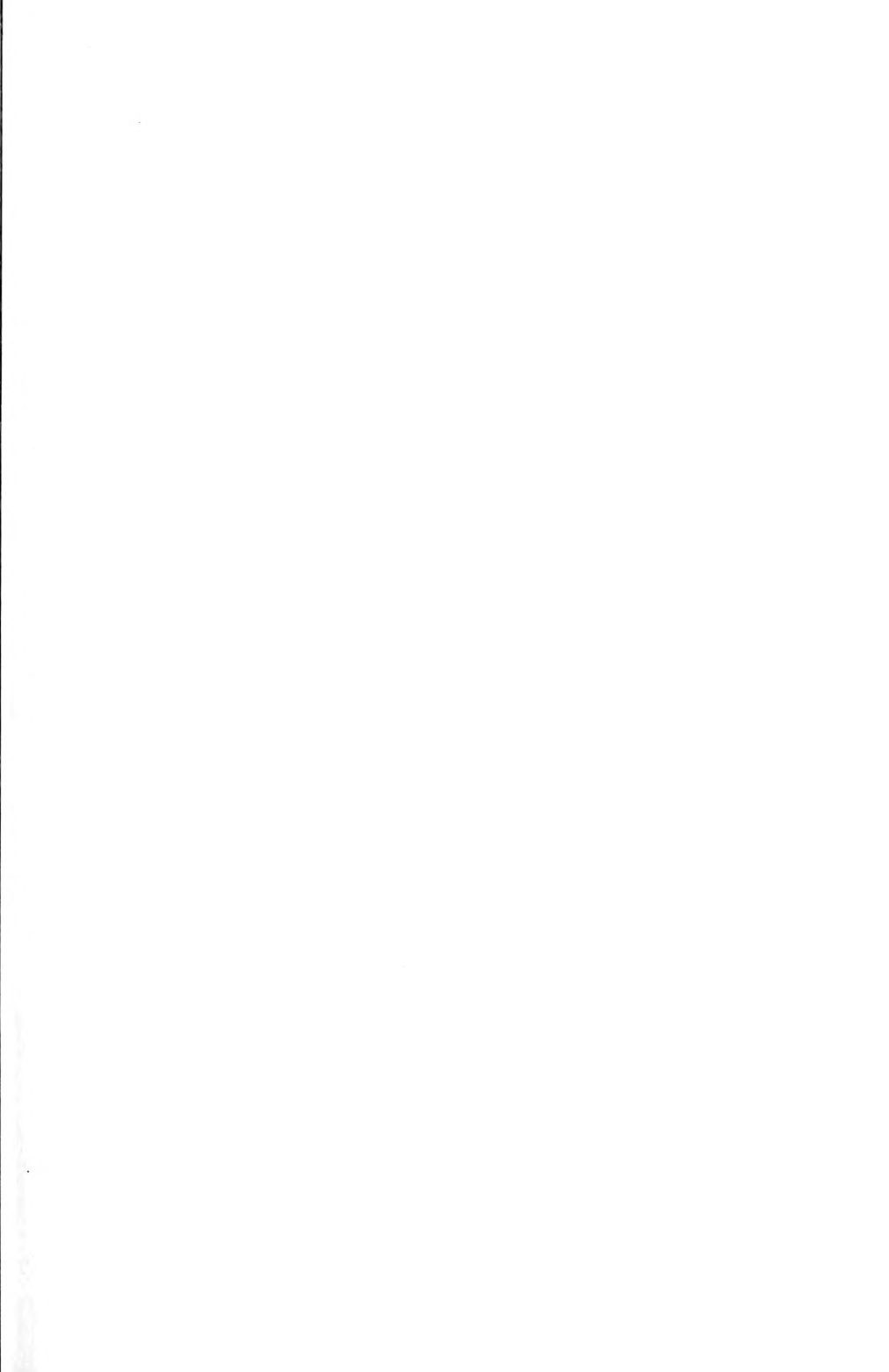
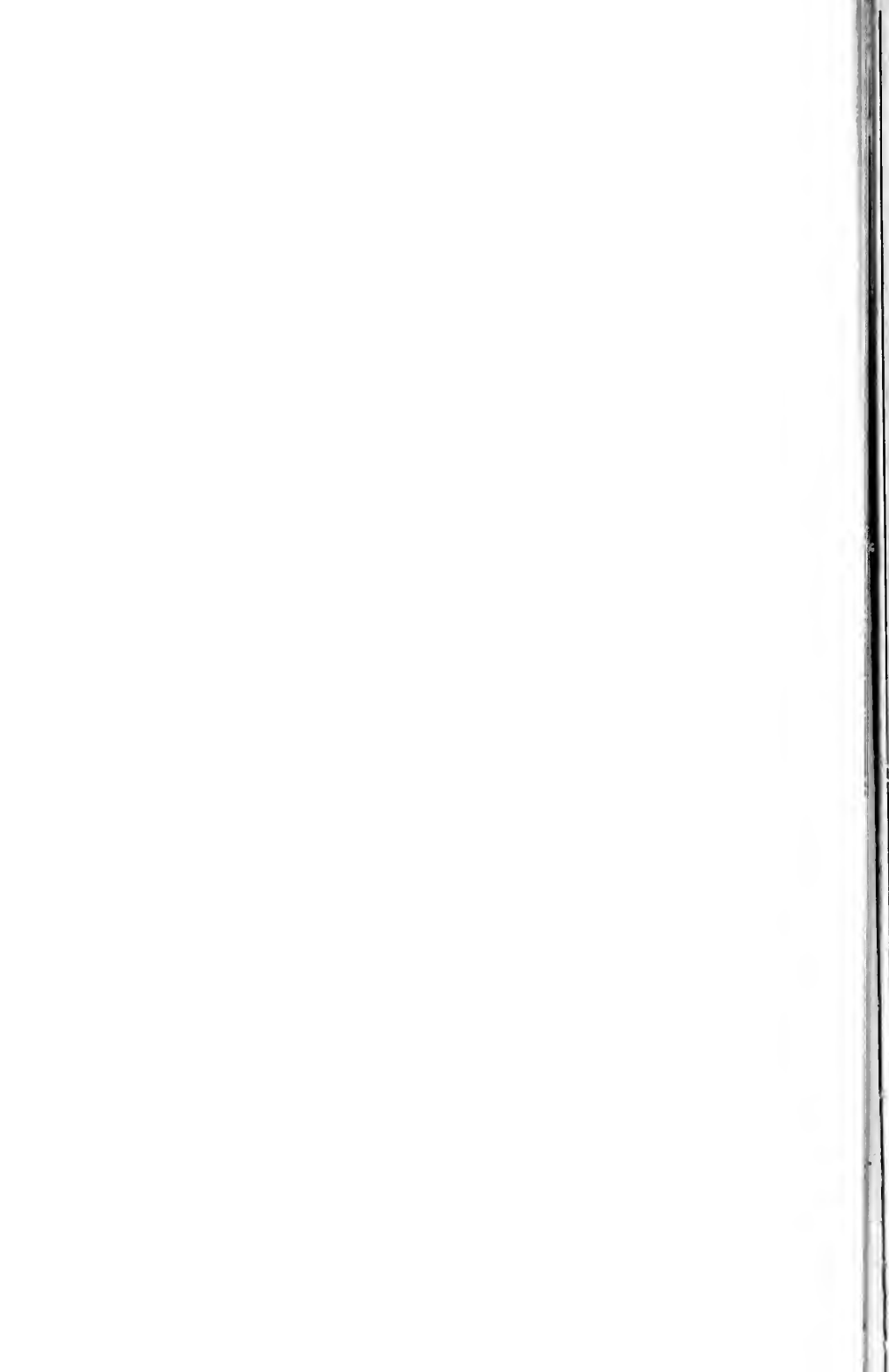


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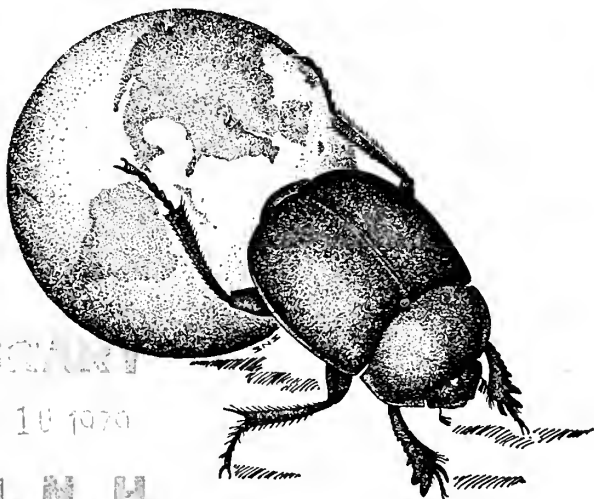
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THE TAXONOMIC POSITION OF THREE NORTH-WEST INDIAN
SPECIES COMMONLY REFERRED TO THE GENUS
PYRAUSTA SCHRANK (LEPIDOPTERA: PYRALIDAE)

H. S. Rose and H. R. Pajni

Abstract.—Three species of subfamily Pyraustinae referable to the unrevised genus *Pyrausta* Schrank were collected from North-West India between November 1972 and November 1974. A critical examination of these species leads to the erection of a new genus *Rattana* with type species *P. euryphaea* Meyrick and the description of a new species, *Coclebotys mutuuri*. The characterization of the new genus and the description of the new species are recorded.

Introduction

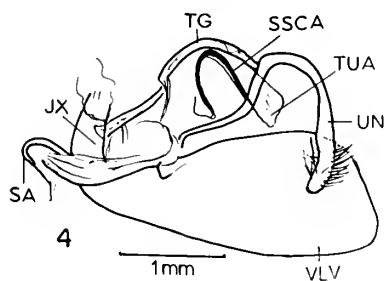
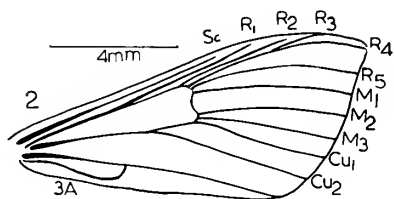
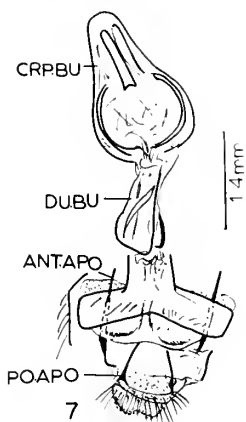
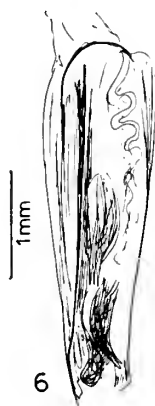
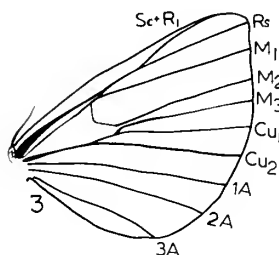
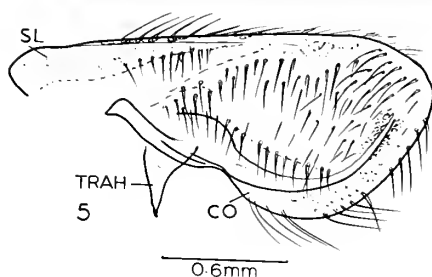
The authors collected ninety two species of subfamily Pyraustinae from North-West India between November 1972 to November 1974. Out of these, three species, as followed through Hampsonian key (1896, 1898), are referable to the old *Pyrausta* Schrank. This genus, however, has been recently found to contain very heterogeneous material and has been divided into two sections, with and without a frenulum hook, restricting genus *Pyrausta* to the section with a frenulum hook and with *P. cingulata* (Linnaeus) as its type species. Munroe (1950, 1958, 1958a) and Munroe and Mutuura (1968c, 1969a, 1969c, 1970a, 1971) have revised the other section and erected several new genera based on other species.

One of three species in our possession, *machoeralis* Walker is referable to the genus *Pyrausta*, as restricted by Munroe (1950). The second species

Abbreviations

1A, First anal vein; 2A, Second anal vein; 3A, third anal vein; ANT.APO, Anterior apophyses; CO, Costa; CRN, Cornuti; CRP.BU, Corpus bursae; Cu₁, First Cubital vein; Cu₂, Second cubital vein; DU.BU, Ductus bursae; JX, Juxta; M₁, First median vein; M₂, Second median vein; M₃, Third median vein; PO.APO, Posterior apophyses; R₁, First radial vein; R₂, Second radial vein; R₃, Third radial vein; R₄, Fourth radial vein; R₅, Fifth radial vein; Rs, Radial sector; SA, Saccus; Sc, Subcosta; Sc + R₁, Stalk of Sc and R₁; SIG, Signum; SL, Sacculus; SSCA, Subscaphium; TG, Tegmen; TRAH, Half transtilla; TU.A, Tuba analis; UN, Uncus; VIN, Vinculum; VLV, Valva.

Figs. 1-7. *Rattana euryphaea*, 1. photograph of adult; 2. forewing; 3. hindwing; 4-6. different parts of male genitalia; 7. female genitalia.



is clearly congeneric with *coclesalis* Walker the type species of the monotypic genus *Coclebotys* (Munroe and Mutuura, 1969c) but is distinctly different from the former and also from all the species described under *Pyrausta* Schrank, and hence a new species. The third species *Pyrausta euryphaea* Meyrick is also referable to the section lacking the frenulum hook but it does not go under any of the genera erected or revalidated by Munroe (1950, 1958, 1958a) and Munroe and Mutuura (1968, 1968a, 1968b, 1968c, 1969, 1969a, 1969b, 1969c, 1970, 1970a, 1971, 1971a). Accordingly a new genus *Rattana* with *Pyrausta euryphaea* Meyrick (new name for *Botys signatalis* Walker, preoccupied) as its type species is proposed. The diagnosis of the genus *Rattana* and a complete description of *Coclebotys mutuuri*, n. sp., are here presented. The terminology for different parts of genitalia has been adopted from Klots (1970).

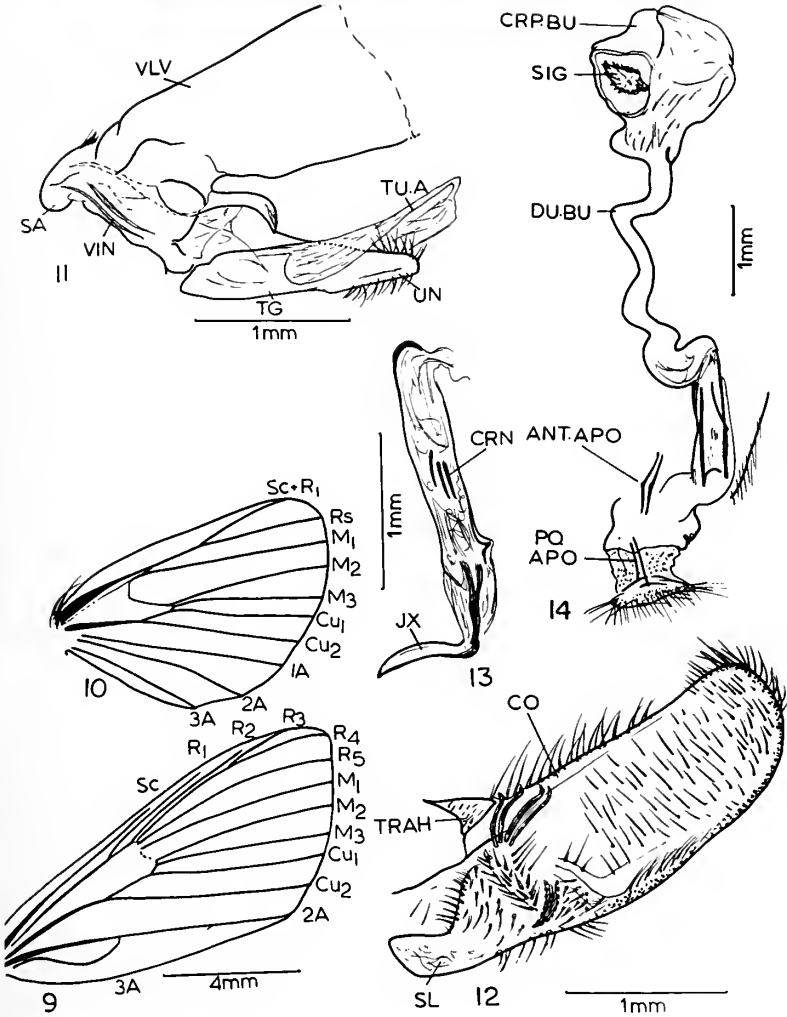
Rattana new genus
(Figs. 1-7)

Type species: *Pyrausta euryphaea* Meyrick Exot. Micr., 4, p. 318 (1932).

Labial palpus porrect and straight; third joint covered with scales from second segment. Maxillary palpus strongly dilated with scales. Frons rounded. Antenna simple, shorter than fore wing. Fore wing with vein R_1 arising from very well before anterior angle of cell; R_2 approximated to R_{3+4} ; R_5 curved and approximated to R_{3+4} ; M_2 , M_3 and Cu_1 from posterior angle of cell. Hind wing with outer margin not excised below apex; discal cell one-third the length of cell; Rs anastomosing with $Sc + R_1$ beyond cell for some distance; M_2 and M_3 closely approximated at base for some distance; Cu_1 from lower angle of cell; frenulum hook absent.

Male genitalia.—Uncus very long, strongly curved, with basal half narrow and distal half dilated and spoon-shaped, dorso-distal and ventro-distal surfaces fringed with setae, extreme tip naked; gnathos absent; tuba analis much shorter than uncus; scaphium not developed; subscaphium strongly sclerotized, supporting tuba analis throughout its length; tegumen arched, roughly as broad as long and strongly sclerotized; vinculum produced anteriorly into a well sclerotized saccus; saccus short. Valva long, the costal margin greatly arched and the saccular margin straight, rounded distally; costa broadly inflated, supported by thin sclerotized lines; sacculus conspicuous; harpe missing. Transtilla with each half sharply triangular, being

→



broad at costa and pointed at apex, weakly sclerotized; juxta more or less rectangular. Aedeagus long, broad at anterior end and slightly narrow posteriorly; vesica armed with two or three spinose patches.

Female genitalia.—Corpus bursae exceptionally reduced, more or less irregular in outline and completely membranous; signum absent; ductus bursae quite long, with a membranous dilation near anterior end and posterior portion sclerotized; anterior apophyses long, each with a triangular thickening near base, base sharply pointed; posterior apophyses short. Ovipositor lobes narrow, setose with long and short setae.

Coclebotys mutuuri n. sp.

(Figs. 8–14)

Holotype.—♀, Uttar Pradesh: Dehra Dun, 21st September, 1973 (H. S. Rose), from fluorescent tube.

Allotype.—♂, same data. Holotype pinned and allotype slides (i.e. wings and genitalia) in Zoological Museum, Entomological Section, Department of Zoology, Panjab University, Chandigarh (India).

Head.—Vertex covered with light ochreous scales and with a whitish tinge; frons oblique and somewhat flattened, smoothly scaled with ochreous scales, scales along inner margins of eyes white. Antenna filiform, shorter than fore wing; scape covered with light brown scales; flagellum with weak annulations on upper surface, the lower almost naked, slightly compressed in male. Eye large, with a row of ochreous scales behind. Ocellus well developed. Labial palpus porrect, exceeding head by less than length of latter; first segment and a small basal portion of second segment on ventral surface covered with white scales, the remainder being fulvous scaled; base of third segment hidden by scales of second segment. Maxillary palpus prominent, strongly dilated with brownish scales distally. Proboscis large, covered with white scales at base. Posterior end of head adorned with long and erect ochreous brown scales, the latter surrounding the white ones.

Thorax.—Ochreous brown dorsally; white ventrally.

Forewing.—Costal margin curved near apex; apex rounded and narrowly acute; termen oblique and somewhat curved; tornus obtuse; anal margin curved near base. Ground color ochreous brown, with costal and outer area slightly darker; a wavy antemedial line from costa to inner margin; a discocellular speck present; a postmedial line from anterior to posterior margin, strongly excurved between M_1 and Cu_1 ; marginal fringe ochreous brown. Discal cell slightly less than half the length of wing. R_1 from before anterior angle of cell; R_2 from upper angle of cell, approximated to R_{3+4} ; R_3

and R_4 stalked; R_5 not approximated to R_{3+4} ; M_1 from somewhat behind upper angle. M_2 , M_3 and Cu_1 from lower angle of cell, fairly spaced around the angle; Cu_2 from cell at two-third the length of cell; 3A making loop with 2A at base.

Hindwing.—Anterior margin straight; apex, termen and tornus rounded. Ground color ochreous brown; outer-marginal area with fuscous suffusion; a postmedial line from R_s to vein Cu , excurved between M_2 and Cu_2 ; marginal fringe ochreous brown. Discal cell less than half the length of wing; discocellular straight and oblique; cell closed. M_2 , M_3 and Cu_1 from posterior angle of cell; M_2 and M_3 closely approximated at base; Cu_2 from cell at two-third the length of cell; three anals present.

Legs.—Clothed with white scales; tibia of prothoracic leg covered with fuscous scales; outer anterior and posterior spurs of male hind tibia minute; outer spur of mid tibia of male and all outer spurs of female about two-third the length of inner spurs.

Abdomen.—Ochreous brown dorsally; pure white ventrally.

Male genitalia.—Uncus relatively reduced, somewhat triangular and rounded at extreme end, heavily setose with anteriorly directed setae; gnathos present; tuba analis longer than uncus; scaphium not developed; subscaphium thin strap-like; tegumen parallel sided posteriorly and well sclerotized; vinculum produced anteriorly into a short saccus. Valva long and of moderate width, costal and saccular margins almost parallel, tip unsymmetrically rounded; costa weakly inflated; sacculus differentiated and carrying a rounded setose lobe, the latter partly underlying the basal part of harpe; harpe represented by a setose lobe, bearing four dorsally directed scale-like strong setae. Transtilla relatively reduced, with each half triangular; juxta moderately stout, with its walls well sclerotized. Aedeagus long and slender, walls well sclerotized, with a short conical projection from a strap-like thickening of aedeagal wall; vesica with three well defined cornuti, along with strap-like thickenings at posterior end.

Female genitalia.—Corpus bursae bag-like and with an irregular boundary; signum with its margin serrate, lateral angles somewhat produced and medial angles rounded; ductus bursae fairly long, strongly sclerotized at the proximal portion; anterior apophyses long and thickened near middle; posterior apophyses short and stout; ovipositor with relatively narrow lobes, each bearing macro and micro setae.

Alar expanse.—Male: 28 mm. Female: 22 mm. to 27 mm.

Paratypes.—5 ♀♀, same data as type, collected between 1.9.1973 to 21.9.1973. (Zoological Museum, Entomological Section, Department of Zoology, Panjab University, Chandigarh, India.)

Acknowledgment

The authors are much indebted to Mr. P. E. S. Whalley and Mr. M. Shaffer of the British Museum (Natural History) London, for the identification of *Pyrausta euryphaea* and for supplying relevant literature.

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EFFECT OF LOW HOST DENSITY ON OVIPOSITION BY LARVAL PARASITOIDS OF THE ALFALFA WEEVIL¹

Robert V. Dowell^{2,3}

Abstract.—I examined the effect of different host densities at low host: parasitoid ratios (1:1–6:1) on parasitism by four larval parasitoids of the alfalfa weevil in the laboratory. The mortality inflicted was independent of changes in host density. This is due to the short handling times (<5 sec) of the *Bathyplectes* spp. and to the ability of *Tetrastichus incertus* (Ratzeburg) to parasitize only 4–5 hosts/day.

Introduction

The alfalfa weevil, *Hypera postica* (Gyllenhal) is one of the most important pests of alfalfa in the United States. Since 1957 it has been the object of a biological control effort by the U.S.D.A. and cooperating states. A total of seven parasitoid species utilizing various developmental stages of the weevil have been established and credited with reductions in alfalfa weevil numbers in the Northeast (Dysart and Day 1976).

The current emphasis on pest management models for the alfalfa weevil system has required a greater understanding of the facts influencing host-parasitoid interactions and how these interactions affect the ability of the parasitoids to stabilize host numbers (Latheef et al. 1977; Yeargan and Latheef 1977). Previous studies with *Bathyplectes anurus* (Thompson)⁴ and *Bathyplectes curculionis* (Thompson)⁴ in open-choice experiments showed no relationship between the various host densities exposed (2, 4, 8, 16 and 32) and the mortality inflicted by the parasitoids (Latheef et al. 1977; Yeargan and Latheef 1976). Thus both parasitoids appear to satisfy the definition of a density-independent mortality factor (van den Bosch and Messenger 1973) and as such are incapable of stabilizing host numbers. Yet *B. curculionis* is credited with substantial biological control of the alfalfa weevil in several sections of the United States (van den Bosch 1971; Michelbacher 1940).

Here I report the results of my investigations into the relationship between

¹ Coleoptera: Curculionidae.

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⁴ Hymenoptera: Ichneumonidae.

host density and parasitism by the 4 larval parasitoids of the alfalfa weevil: *B. anurus*, *B. curculionis*, *Bathyplectes stenostigma* (Thompson) and *Te-trastichus incertus* Ratzeburg.⁵ In particular, I dealt with very low host: parasitoid ratios (1:1–6:1) to determine how the parasitoids responded to changes in host density at such levels.

Methods and Materials

I reared host larvae from eggs of field collected adults (Dowell 1977a). Twenty-four hours prior to their being exposed to parasitoids, I placed 1–6 host larvae on three 7-cm-long alfalfa stems in a cotton plugged 5-cm glass vial to allow feeding and the accumulation of feces. Host larvae and their feces stimulate searching behavior in both the *Bathyplectes* spp. (Dowell 1977, McKinney and Pass 1977) and *T. incertus* (Dowell and Horn 1977). The 2nd instar hosts used for the *Bathyplectes* spp. and the 3rd instar hosts used for *T. incertus* are within the preferred host range of each parasitoid (Dowell 1977; Dysart and Day 1976).

The source and care of the various parasitoids are described elsewhere (Dowell 1977; Dowell and Horn 1976). Prior to use, each female was held for 24 hours without hosts and then 24 hours with hosts to allow for ovary maturation (all species), to prevent an excessive accumulation of eggs in the lateral oviducts of the *Bathyplectes* spp. and to allow *T. incertus* to feed on host exudates from ovipositional wounds (Dowell 1978). Each mated female was then exposed to different number of hosts daily for 2–5 successive days. Care was taken to avoid having the total number of hosts exposed exceed the expected fecundity of the parasitoid species (Dowell 1977). Host larvae were exposed to individual parasitoids in 10 × 10 × 9 cm plastic containers (Dowell 1977) for 24 hours in a Percival environmental chamber held at 21°C and 12 hour photophase. After use, all parasitoids were dissected to be certain that their ovaries were functional (Dowell 1976), and only those females with functional ovaries were included in the data analysis. A minimum of four replicates/density/species were run. After exposure the host larvae were reared until pupation to determine whether they were parasitized. The data for each host density were averaged by parasitoid species and mortality was expressed as k-values ($k = \log_{10} \text{initial \#} - \log_{10} \text{survivors}$) (Varley and Gradwell 1965). The effect of host density on mortality (k-values) was examined by use of regression analysis.

A fungal disease similar to that described by Dysart and Coles (1971) killed most of the larvae exposed to *B. stenostigma*.

Results and Discussion

Table 1 shows the results of the regression analysis of the k-values on host density for each parasitoid. There was no significant ($P < 0.05$) affect

⁵ Hymenoptera: Eulophidae.

Table 1. Results of regression analyses of k-values (y) of the larval parasitoids on alfalfa weevil density (x).

Parasitoid species	Regress. coeffs.	Intercept	Standard error of estimate	r	t-value H ₀ : b = 0
<i>B. anurus</i>	-0.01	0.39	0.24	-0.05	-0.17*
<i>B. curculionis</i>	0.04	0.14	0.18	0.31	0.05*
<i>T. incertus</i>	-0.01	0.44	0.10	-0.25	0.42*
<i>B. stenostigma</i>	0.15	0.15	0.11	0.98	5.01†

* Not significantly different from b = 0 at $P = 0.05$ as determined with a t-test.

† Significantly different from b = 0 at $P = 0.05$ as determined with a t-test. However there were only 4 data points for this analysis; one replicate at each of 4 densities.

exerted by changes in host density on the mortality inflicted by *B. anurus*, *B. curculionis* or *T. incertus*. Only the mortality inflicted by *B. stenostigma* significantly ($P > 0.05$) changed with changes in host density. However, the previously mentioned disease limited this data analysis to the 1 replicate that survived at each of 4 densities. Previously I (Dowell 1977; 1978) have shown that the biology and reproductive tactics of *B. stenostigma* differ little from its congeners. Based upon these previous studies, I feel that *B. stenostigma* probably responds to changes in host density in a manner similar to its congeners and that the small number of replicates analyzed were insufficient to show this.

The density-independent response of *B. anurus* and *B. curculionis* to changes in host density at these low host:parasitoid ratios agree with previous studies using greater ratios (5:1-100:1) (Barnety et al. 1977; Latheef et al. 1977; Yeargan and Latheef 1977). That *T. incertus* also responded in a density-independent manner is surprising since its reproductive biology differs greatly from that of the *Bathyplectes* spp. (Dowell 1978; Dowell and Horn 1977). Recent studies have shown that the field mortality inflicted by *B. anurus* and *B. curculionis* in Ohio (Lewis 1977) and by *B. curculionis* and *T. incertus* in Ontario (Harcourt et al. 1977) is independent of changes in host density.

I believe that the density-independent response of the *Bathyplectes* spp. and *T. incertus* to changes in host density have different origins but that both can be explained by the effect of several biological traits on the disc equation (1) of Holling (1959).

$$N_a = \frac{a T_t N_o}{1 + a T_h N_o} \quad (1)$$

Where:

N_a = Number of hosts parasitized

a = area of discovery

$$\begin{aligned}T_t &= \text{exposure time} \\T_h &= \text{Handling time/host} \\N_o &= \text{Number of hosts available.}\end{aligned}$$

The handling time for the *Bathyplectes* spp. is <5 sec/larva (Dowell 1977) making it approximately equal to zero when compared to the exposure time of 12 hr. When this happens; equation 1 can be reduced to the following:

$$N_a = aT_tN_o \quad (2)$$

The numbers of hosts parasitized now becomes a linear function of the number of hosts available as 'aT_t' is a constant in this equation. According to both this study and others cited herein, the slope of this linear function does not significantly differ from zero.

The handling time for *T. incertus* is >23 min/larva (Horn 1970) and is large enough to keep equation from reducing. When the average number of hosts at each density is fitted to the disc equation by the method described by Holling (1959) and Messenger (1968) the result is equation 3.

$$N_a = \frac{0.68N_o}{1 + 0.07N_o} \quad (3)$$

According to equation 3, *T. incertus* should show a density-dependent response to changes in host numbers until all the available eggs have been laid. I believe that *T. incertus* is capable of parasitizing an average of only 4–5 hosts/day. This low figure is limited in two manners. The first is that egg production in *T. incertus* is dependent upon a continual supply of proteins gathered by feeding on ovipositional wounds on the host (Dowell 1978). This combined with the low number of ovarioles/ovary (n = 12) (Dowell 1978) limit the number of eggs formed/day. In addition *T. incertus* lays an average of 5–6 eggs/host (Streams and Fuester 1967) further restricting the number of host larvae it can parasitize on a daily basis. The final result is that a density-dependent process appears density-independent due to the limited number of hosts the parasitoid can parasitize on a daily basis.

The density-independent mortality inflicted by the larval parasitoids of the alfalfa weevil, whether based upon the rapid handling time/larvae or the limited number of larvae that can be parasitized/day, make them incapable of stabilizing host numbers. While their presence does increase host mortality, they alone are not responsible for long-term decreases in host numbers.

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MITE PREDATORS IN EASTERN NEW YORK
COMMERCIAL APPLE ORCHARDS¹

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Abstract.—A survey for predators of apple leaf-feeding mite species was made during mid-summer of 1975, 1976, and 1977. Apple leaves were collected from 36 commercial orchards throughout the 10 major fruit-growing counties of Eastern New York. The phytoseiid mite predators *Amblyseius fallacis* (Garman), *Typhlodromus pomis* (Parrott), and *Typhlodromus* sp. were found in 26, 2, and 1 of the orchards, respectively. The stigmatiid *Zetzellia mali* (Ewing) was found in eight of the orchards, while the coccinellid beetle *Stethorus punctum* LeConte was found in one. Results of this survey suggest that Eastern New York apple growers could utilize certain of these mite predators in integrated mite control programs similar to those developed in other areas.

Introduction

Recent emphasis on more efficient utilization of chemical pesticides in deciduous orchards has encouraged the development of integrated mite control programs employing mite natural enemies in addition to chemical and cultural control methods (Glass, 1975). The development of widespread resistance to organophosphate insecticides among predatory mites of the family Phytoseiidae (Croft and Brown, 1975) has provided much of the impetus for such programs.

Dean (unpublished manuscript) listed four species of plant-feeding mites on apple trees in the Hudson Valley including the European red mite, *Panonychus ulmi* (Koch), twospotted spider mite, *Tetranychus urticae* Koch, clover mite, *Bryobia praetiosa* Koch, and apple rust mite, *Aculus schlechtendali* (Nalepa). The aforementioned species plus the McDaniel spider mite, *Tetranychus mcdanieli* McGregor, have been reported (Brann, 1976) in the Champlain Valley.

Dean (unpublished manuscript) listed the ladybird beetle, *Stethorus punctum* LeConte, as the most common mite predator in the Hudson Valley and reported that two bugs *Hyaloides vitripennis* (Say) and *Orius insidiosus* Say, known to feed on the European red mite had been largely eliminated from most orchards by DDT sprays. Dean also found predaceous phyto-

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seiids but considered their influence slight. Specimens of the predaceous stigmatid, *Zetzellia mali* (Ewing), were collected during 1969 from the Hudson Valley Laboratory orchards by Dr. Dean and identified by Dr. E. W. Baker.

Phytoseiid mite predators were found where reduced rates of miticides were used in large plot mite control studies conducted during 1974 in the Champlain Valley. Subsequent trials in both the Hudson and Champlain Valleys indicated that the phytoseiids were providing biological control of the European red mite (Weires, unpublished data). A limited survey for mite predators was conducted in Ulster and Clinton counties during 1975, while the survey was expanded during 1976 and 1977 to include these as well as eight other counties (Fig. 1) throughout Eastern New York.

Materials and Methods

Leaf samples were collected from six orchards in Clinton and Ulster counties in 1975, from 22 orchards throughout Ulster, Clinton, Saratoga, Orange, Rockland, Putnam, and Greene counties in 1976, and from twelve orchards in Columbia, Dutchess, Rennselaer, Rockland and Orange counties in 1977. Orchards were randomly selected with the help of Cooperative Extension fruit agents. Sample size varied, but at most locations four to eight blocks which included at least two varieties (one of them McIntosh) and ranged in size from 5–15 acres were sampled by collecting 10 leaves/tree from five trees in each block. More intensive sampling was conducted where greater precision was required to determine predator-prey ratios. The number of samples/orchard, leaves/sample, and leaves/tree, as well as the sampling date and location are presented in Table 1.

Mites were brushed from the leaves onto a glass plate coated with glue using a mite brushing machine (Henderson & McBurnie, 1943). All mite species and stages were counted and growers were sent a report of the counts. Predatory mites were carefully removed from the plates, placed in 95% EtOH, and mounted in PVA modified Heinz medium.

Dr. Chand Watve (Geneva, NY) helped collect, mount, and identify the phytoseiids during 1975, while in 1976 and 1977 the phytoseiids were mounted and identified by Mr. Smith and confirmed by Dr. Watve. Collections of the stigmatidae were compared with original specimens determined by Dr. Baker or sent to Dr. Watve. The coccinellids were determined by Dr. John Leeper (Geneva, NY).

Results and Discussion

Three species of phytoseiid predators were found. *Amblyseius fallacis* (Garman) was the predominant species. *Typhlodromus pomi* (Parrott) was found in one orchard during 1975 and 1976 (Table 1). Another unidentified *Typhlodromus* species was also found in one orchard in 1975.

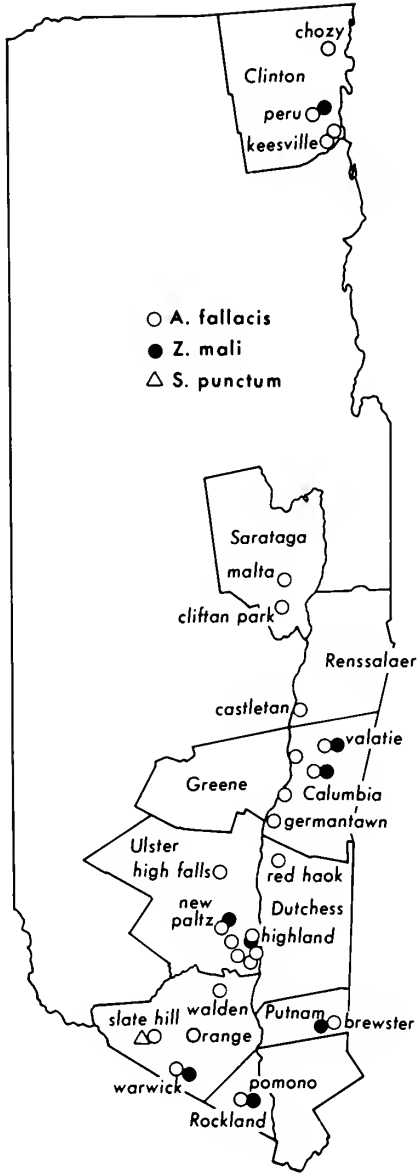


Fig. 1. Location of commercial apple orchards surveyed for mite predators in Eastern New York, 1975–1977.

Amblyseius fallacis was found in 5 of the 6, 14 of the 22, and 11 of the 12 orchards surveyed in 1975, 1976, and 1977, respectively. *Zetzellia mali* was found in three of the orchards surveyed each season. *Stethorus punctum* was found in the same orchard in both 1976 and 1977.

Table 1. Mite predators in Eastern New York Commercial Apple Orchards—1975–1977.

Date sam- pled	Orchard	City or village	County	No. sam- ples	No. leaves/ sample	No. leaves/ tree	Predator species		
							<i>A. fal- lacis</i>	<i>Z. mali</i>	<i>S. punc- tum</i>
1975									
7/29	A	New Paltz	Ulster	48	25	25	X ¹	X	O
7/29	B	Clintondale	Ulster	4	50	25	X	O	O
7/29	C	High Falls	Ulster	4	50	25	X	O	O
7/29	D	Highland	Ulster	39	25	25	X	X	O
7/29	E	Keesville	Clinton	48	25	25	X	O	O
7/29	F	Peru	Clinton	4	25	25	O	X	O
1976									
7/22	G	Brewster	Putnam	4	50	25	X	X	O
7/26	H	Pomona	Rockland	12	50	25	O	O	O
8/3	I	Slate Hill	Orange	5	50	10	O	O	X
8/3	J	Warwick	Orange	5	50	10	X ²	X	O
8/18	K	Walden	Orange	6	50	10	X	O	O
8/3	L	Walden	Orange	8	50	10	X	O	O
8/2	M	Plattekill	Ulster	4	50	10	O	O	O
8/2	N	Plattekill	Ulster	4	50	10	X	O	O
8/2	O	Marlboro	Ulster	4	50	10	X	O	O
7/20	P	Milton	Ulster	40	25	25	X ¹	O	O
8/2	Q	New Paltz	Ulster	5	50	25	X	O	O
6/24	D	Highland	Ulster	36	25	25	X	X	O
8/2	R	Ulster Park	Ulster	4	50	10	O	O	O
7/22	S	Athens	Greene	4	50	10	O	O	O
7/22	T	Malta	Saratoga	4	50	25	X	O	O
7/22	U	Clifton Park	Saratoga	4	50	25	X	O	O
7/22	V	Rexford	Saratoga	4	50	25	O	O	O
7/13	E	Keesville	Clinton	52	25	25	X	O	O
8/13	W	Peru	Clinton	4	50	10	X	O	O
8/13	X	Chazy	Clinton	4	50	10	O	O	O
8/13	Y	Chazy	Clinton	4	50	10	O	O	O
8/13	Z	Chazy	Clinton	2	50	10	X	O	O
1977									
8/1	AA	Claverack	Columbia	6	50	10	O	O	O
8/2	BB	Red Hook	Dutchess	6	50	10	X	O	O
8/2	CC	Germantown	Columbia	8	50	10	X	O	O
8/2	DD	Greenport	Columbia	8	50	10	X	O	O
8/3	EE	Red Hook	Dutchess	4	50	10	X	O	O
8/4	I	Slate Hill	Orange	8	50	10	X	O	X
8/4	FF	New Hampton	Orange	4	50	10	X	O	O
8/4	H	Pomona	Rockland	8	50	10	X	X	O
8/5	GG	Valatie Co	Columbia	8	50	10	X	X	O
8/5	HH	Kinderhook	Columbia	6	50	10	X	O	O
8/5	II	Castleton	Rensselaer	6	50	10	X	O	O
8/5	JJ	West Ghent	Columbia	4	50	10	X	X	O

X = present. O = absent.

¹ Several *Typhlodromus pomi*.² Several *Typhlodromus* sp?.

Amblyseius fallacis was found where a variety of orchard spray programs were used, whereas *T. pomi* and *Z. mali* were only found in young, seldom-sprayed orchards or in older orchards being brought back into production or receiving a very minimal spray program. *Stethorus punctum* was found in an orchard which received regular sprays, but in which European red mite populations exceeded five mites/leaf at the time of sampling.

Knisley and Swift (1972) found eight species of phytoseiid mite predators in New Jersey apple orchards. *Amblyseius fallacis* was the predominant species in orchards receiving pesticide sprays while *Typhlodromus longipilus* Nesbitt was found less frequently. *Typhlodromus pomi* was the most common phytoseiid in abandoned orchards. The stigmatids *Z. mali* and *Agistemus fleschneri* (Summers) were found in both abandoned and commercial orchards (Knisley and Swift, 1972).

Growers throughout Eastern New York should be able to utilize *A. fallacis* in integrated mite control programs similar to those developed for other areas (Swift, 1968; Holdsworth, 1974; Croft, 1975). This is in contrast to the situation in Western New York where both *A. fallacis* and *Typhlodromus pyri* Scheuten are found with *T. pyri* predominant (Watve and Lienk, 1976 and pers. communication). The absence of *T. pyri* in our collections is considered a benefit (1) because of the threat it poses for *A. fallacis* through interspecific competition; (2) because of its low level of tolerance to the most commonly used organophosphate insecticides (Watve and Lienk, 1976); and (3) because there is some question as to its predatory effectiveness (Croft, 1976).

Utilizing *Z. mali* in an integrated program does not appear promising. *Zetzellia mali* is apparently susceptible to present pesticide programs. Recent work also suggests that because of spatial heterogeneity coupled with lack of feeding on female tetranychids, *Z. mali* may not be able to control phytophagous mites below economic damage levels (Santos, 1976). In addition Croft and McGroarty (1977) have observed that *A. fallacis* seemed unable to express its normal reproductive and predation potential in orchards where *A. fleschneri* and *Z. mali* were present at similar densities to *A. fallacis*.

Stethorus punctum was found in only one orchard during our collections. Croft and McGroarty (1977) reported that *S. punctum* occurred very sporadically in Michigan apple orchards but that its occurrence was unrelated to pesticide use patterns. Growers in the southwestern portion of the Hudson Valley should be able to utilize *S. punctum* in an integrated mite control program but would probably have to adapt the Pennsylvania integrated mite control practices (Tetrault et al., 1977) designed to protect *Stethorus*.

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STRATEGIES OF GALL FORMATION IN
PEMPHIGUS APHIDS^{1, 2}

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Introduction

This is a study of the various aspects of the strategies of gall formation by two species of aphids which form galls on the leaves and petioles of the Eastern Cottonwood, *Populus deltoides*. *Pemphigus* galls are initiated when a young stem mother or fundatrix (the name for the first parthenogenetic generation after the sexual generation) begins feeding on the newly emerging leaves of *Populus*. On Long Island, the two common gall-forming species on cottonwood are *Pemphigus populicaulis* Fitch and *P. populitransversus* Riley. These induce "oblique" and "transverse" galls, respectively. The *oblique* gall is formed by a swelling and twisting of the leaf at the point where the blade meets the petiole. The *transverse* gall, by contrast, is formed entirely on the leaf petiole. In each case, feeding by the fundatrix induces changes in the growth of the plant tissue, resulting in a chamber enclosing her. The parthenogenetic offspring of the mature fundatrix usually remain within the gall until after a final molt that, in all cases, results in winged individuals. These winged forms (alate fundatrigeniae, called "alates" for short in this paper) migrate to the roots of a secondary host plant (members of the Cruciferae or Compositae). After one or more parthenogenetic generations on the secondary host, winged forms ("sexuparae") are produced that return to the primary host (*Populus*) and give birth parthenogenetically to sexual forms. Each fertilized female deposits, in cracks in the bark of the tree, a single egg which in turn develops into a fundatrix, completing the life cycle (Harper 1959). The exact timing of these life history stages for *P. populicaulis* and *P. populitransversus* will be discussed later in this paper.

Initiation of *Pemphigus* galls has been observed only on young, newly unfolding leaves. *P. deltoides* produces leaves continuously throughout the summer; early leaves are preformed in the winter bud and morphologically distinct late leaves are formed from leaf primordia after the expansion of the early leaves (Kozlowski 1971). As a result, feeding sites for young fundatrices are continuously available from spring until late summer. However, once the fundatrix initiates a gall, it does not appear to change its feeding site.

For purposes of this paper, I shall define "gall position" as one plus the number of leaves on a shoot preceding (older than) the leaf bearing the gall.

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For example, if the gall position is "6," then the gall is located on the sixth leaf of the shoot, counting from the base of the shoot.

Obviously, the proximal causes of a given gall position are the time the fundatrix nymph emerges and initiates the gall, the time of bud break of the shoot, and the subsequent rate of leaf expansion of the shoot. The ultimate causes of gall position, that is, the selective pressures affecting the timing of gall initiation, are discussed in this paper.

Whitham (1974) first considered the adaptive significance of the position of *Pemphigus* galls on cottonwoods. He showed that galls sharing the same leaf were generally smaller than single galls, and argued that the aphids were resource (sap) limited. He found a significant correlation of gall size with leaf size for oblique and transverse galls, and also showed that galls of both species are found on larger-than-average leaves. He suggested that the obliques may achieve this through the timing of gall formation and the transverse through the "choice" of longer shoots bearing larger leaves.

My preliminary observations on one tree showed that of 129 oblique galls, 97 (75.2%, with 95% confidence levels 66.5–82.8%) were found on the largest leaf of their shoot. However, of 154 transverse galls, only 38 were found on the largest leaf (24.7%, limits 19.1–33.0%). The correlation of leaf length with gall diameter was 0.87 ($n = 129$) for oblique galls and 0.39 ($n = 154$) for transverse galls. This suggested that, to the extent that fitness is related to gall size, leaf length might influence the success of transverse galls less than that of oblique galls.

In this paper a dimorphism in gall position of *P. populitransversus* is demonstrated. Then, the possible factors affecting relative success of these galls are determined with the goal of discovering whether there is differential fitness at different gall positions. Finally, for both *P. populitransversus* and *P. populicaulis*, position is analyzed as a possible response to such selection pressures.

Materials and Methods

Observations and collections were made from cottonwood trees in the vicinity of Stony Brook, Long Island, starting in early May, 1975. Measurements of the cottonwoods were made in the field and galls were removed, tagged, and placed in jars of alcohol. *Populus* measurements included tree height and for shoot samples, the number of leaves on the shoot, gall position, position of the largest leaf, petiole lengths, and leaf lengths. In the laboratory, each gall was measured and its aphid population censused under a dissecting microscope. The numbers of winged forms and individuals in three arbitrarily chosen size classes of nymphs were recorded for all galls. Galls that showed signs of predation or other disturbances were not used for this study.

Relative reproductive success of different fundatrices was estimated by censuses of galls in which some winged forms had developed. This seems to be a reasonable estimate of the reproductive potential of a gall for the season. In a study of six species of *Pemphigus* in Alberta, including *P. populicaulis* and *P. populitransversus*, Harper (1959) found a correlation of 0.99 between the *average number of aphids* emerging from a gall for a given species over the summer and the *average population counts in galls* in a separate sample of that species. I will also assume that, within a species, differences in population counts among galls reflect differences in the number of migrants that could be expected from the galls over the summer.

Dimorphism in the Timing of Gall Initiation in *P. populitransversus*

Gall initiation by *Pemphigus populitransversus* was found to occur at two clearly separate times during the summer of 1975. Gall initiation is first detected as a slight swelling and bending of the petiole at the point where a fundatrix nymph has begun feeding. In this early stage, the young fundatrix is not enclosed and appears as a small black spot in the pocket formed by the swelling and bending of the petiole. Transverse galls first began forming, along with oblique galls, around May 15 on cottonwoods in the vicinity of Stony Brook. At this time, the early leaves of the tree were expanding and provided suitable sites for gall initiation. The trees were checked carefully on successive days, and after two or three days, there was no further gall initiation. Then, on June 15, more transverse galls began forming on the newly formed late leaves. This dimorphism in the timing of gall initiation resulted in a set of galls on the early leaves and a set of galls on the late leaves of the shoots. The early transverse galls had an average position of $6.2 \pm .39$ ($n = 48$), over several trees, while the average position of the late galls was $16.2 \pm .35$ ($n = 85$).

A dimorphism in gall shape, life history, and aphid morphology has been described for this species by Senner and Sokal (1974). The morph they refer to as "*elongate*" produces galls that are more elongate in shape than those of the other morph called "*globular*." The question immediately arose whether the presence of early and late transverse galls was related to the globular-elongate dimorphism. An analysis of the early and late transverse galls confirms the suspected relationship (Table 1). The late galls are larger than the early galls, and more spherical, as shown by the ratios of gall dimensions. The values in Table 1 resemble those of the sample from West Point, Georgia, shown in Table 3 of Senner and Sokal (1974). The early and late galls were significantly different for each character. Corroborating tests were run following methods developed by Senner and Sokal (1974). The gall dimensions and their ratios split a mixed sample of 71 galls into early and

Table 1. Means of gall characters for 39 early and 31 late transverse galls in Stony Brook, New York, 1975.

Gall character	Early transverse	Late transverse	F_s
Length	10.9	14.7	38.9
Width	7.5	14.3	19.4
Depth	8.0	13.4	12.4
Length/width	1.46	1.03	77.2
Length/depth	1.38	1.11	20.5

Note: Measurements are in millimeters. F_s is the sample F -statistic testing differences between the means. All values of F_s are significant at $P < 0.001$.

late classes fairly well. Only two galls would be misclassified by time of gall formation when the sample was split according to gall depth and only 4 galls would be so misclassified on the basis of length/width ratio. It is highly probable that the early and late galls correspond to the elongate and globular morphs, respectively.

Population Sizes in Globular and Elongate Galls

Senner and Sokal (1974) found that globular galls had larger within-gall population sizes than elongate galls. Table 2 summarizes the data on population size for several trees on Long Island. In a pooled sample from several trees, the population size of globular galls was higher than that of elongate galls; the average population size of globular galls was 377.6 ± 19.2 ($n = 60$) compared with 290.9 ± 13.6 ($n = 52$) for elongate galls, for trees on which both types of galls were present. These values were significantly different ($F_s = 10.4 > F_{.005(1,111)}$). For individual trees, the results were somewhat variable (Table 2). The difference in population size between elongate and globular morphs was significant for both tree 4 and tree 8 ($F_s = 9.8 > F_{.005(1,46)}$, $F_s = 7.6 > F_{.025(1,21)}$). For tree 3, the difference in population sizes of the two morphs was not significant ($F_s = .128 < F_{.90(1,24)}$). Thus, average population size is somewhat variable among trees for each morph, but in general, stem mothers of globular galls produce more offspring than those of elongate galls.

Table 2. Mean population size (\pm standard error) of globular and elongate galls for different trees in Stony Brook, New York, 1975.

	Tree 3	Tree 4	Tree 8
Globular	376 ± 46.3 (14)	409 ± 29.0 (29)	454 ± 37.3 (12)
Elongate	357 ± 26.4 (11)	237 ± 20.1 (18)	294 ± 19.1 (10)

Note: Sample sizes (number of galls) in parentheses.

Table 3. Analysis of covariance of population sizes of globular galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation	Sum of squares	df	Mean squares	F_s
Corrected total	1638165.15	73		
Adjusted treatment	212100.79	2	106150.40	13.53***
Regression	1073545.41	6	178924.24	22.82***
Error	509518.67	65	7838.75	
Regression homogeneity	111766.55	12	9313.88	1.24ns
Error for regression homogeneity	397752.13	53	7504.76	

Partial regression coefficients						Adjusted treatment means		
GL	GW	GLP	LAG	GPL	GLL	Tree number		
23.0	30.6	-6.5	4.0	-20.1	-.7	2	3	4
						314.5	478.7	396.3

Correlation matrix							Population size
	GL	GW	GLP	LAG	GPL	GLL	
GL		.618	.008	-.217	-.498	.000	.612
GW			.000	.116	-.327	.200	.684
GLP				.008	.000	.326	-.097
LAG					.000	.299	.131
GPL						.000	-.284
GLL							.009

Note: Treatments are differences among three trees. Gall characteristics used as covariates are: GL—gall length, GW—gall width, GP—gall position, LAG—number of leaves after gall position, GPL—number of galls per leaf, GLL—length of leaf bearing the gall. Significance values are symbolized by ***— $P \leq .001$, **— $.001 P \leq .01$, *— $.01 P \leq .05$, ns— $P > .05$. All correlation coefficients significant at $P \leq .01$ are in italics.

What factors account for the variation in population size among galls within each morph? Can factors relating to the difference in gall position of the two morphs account for the greater population sizes of the globular galls? Also, is there evidence of competition between galls? Such evidence would suggest some limiting factor on population size. I shall address these questions in turn.

The population size of globular galls was used as the dependent variable in an analysis of covariance (Table 3). Gall length, gall width, gall position, the number of leaves after (distal to) the gall position, the number of galls per leaf, and the length of the gall-bearing leaf were used as covariates and the 3 trees sampled served as treatments. The regression was significant and homogeneous over trees. However, the adjusted treatment means were sig-

nificantly different ($F_s = 13.5 > F_{.001(2,65)}$); therefore, the regression does not completely account for the variation in population size among trees.

The partial regression coefficients for gall length, gall width and gall position were significant ($F_s = 19.8 > F_{.001(1,65)}$, $F_s = 23.9 > F_{.001(1,65)}$, and $F_s = 3.86 > F_{.05(1,65)}$, respectively). As noted earlier, population size increased with gall dimensions. However, it decreased with position. Age of the gall may be responsible for this effect, since galls with lower positions will be slightly older and hence more populated than those at higher positions.

There seems to be some competition among galls on the same leaf, as suggested by the significant negative correlation of number of galls per leaf with gall length and gall width, and the negative correlation of number of galls per leaf with population size (significant at $P < 0.025$). The effect of the number of galls on a given leaf or shoot on population size in the galls seems to be realized through the effect of number of galls on gall dimensions.

For tree 2 alone, competition was tested between galls on the same shoot. The number of galls per shoot was seen to increase with the number of leaves on the shoot ($r = .60$, $n = 31$). The regression of population size on the number of galls per shoot, holding the number of leaves constant, was also significantly negative ($F_s = 8.4 > F_{.001(2,65)}$). There would appear to be competition for resources among globular galls on the same shoot.

Gall leaf length was found to increase with gall position; that is, leaves were larger toward the tip of the shoot. However, the length of the leaf did not seem to be important to the success of the gall. Gall leaf length had no significant correlation with population size, or with gall dimensions. Thus, larger populations are found in larger galls and in earlier positions, but this is not related to leaf size.

A similar analysis of covariance was performed for three trees with elongate galls (Table 4). The regression is significant and, in this case, it does account for the difference in the average population sizes of the three trees, since the adjusted treatment means were not significantly different ($F_s = 2.98 < F_{.10(2,39)}$).

Again, gall dimensions correlate highly with population size in the gall, but only the partial regression coefficient on gall width was significant ($F_s = 4.33 > F_{.05(1,39)}$). Gall leaf length, as in the case of globular galls, increases with gall leaf position and does not show a significant correlation with population size or gall dimensions. However, in contrast to the globular case, the gall position correlated positively with population size. To investigate further any effect due to variation in leaf length with position, population size was regressed on gall position, holding gall leaf length constant. This regression was significant ($F_s = 5.37 > F_{.05(1,40)}$). Therefore, in elongate galls, there must be some factor other than leaf size relating to gall position that affects population size.

Table 4. Analysis of covariance of population sizes of elongate galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation			Sum of squares			df	Mean squares		F_s
Corrected total			427501.48			47			
Adjusted treatment			31698.23			2	15849.14		2.98ns
Regression			121292.59			6	20215.43		3.80**
Error			207382.82			39	5317.51		
Regression homogeneity			55584.99			12	4632.08		.82ns
Error for regression homogeneity			151797.83			27	5622.14		
Partial regression coefficients						Adjusted treatment means			
GL	GW	GLP	LAG	GPS	GLL	Tree number			
10.4	33.3	4.5	-1.9	11.1	-.60	3	4	8	
						329.2	285.5	228.1	
Correlation matrix									
	GL	GW	GLP	LAG	GPS	GLL	Population size		
GL		.445	.253	.110	-.198	.156	.430		
GW			.009	.144	-.181	.063	.462		
GLP				-.298	.150	.528	.462		
LAG					.496	.455	-.170		
GPS						.494	.423		
GLL							.276		

Note: See Table 3.

For elongate galls, competition was examined in terms of galls on the same shoot. Surprisingly, the number of galls per shoot correlated positively with population size within a single tree. The number of galls per shoot correlated with shoot length ($r = .496$, $n = 48$). Longer shoots produce numerous and more populated galls for unknown reasons.

To find the causes of the differences in the average population sizes of globular and elongate galls, these morphs were used as treatments in an analysis of covariance (Table 5) with gall length, gall width, gall leaf length, and the number of leaves after the gall as covariates. The two treatments were significantly different for each of these variables. The treatment means of populations sizes were 378 ± 19.2 for globular and 291 ± 13.6 for elongate galls.

As expected, the partial regression coefficients for gall length and gall width were significant ($F_s = 8.7 > F_{.005(1,128)}$, $F_s = 12.0 > F_{.001(1,128)}$). These gall dimensions account for the differences in population size of the two

Table 5. Analysis of covariance of population sizes between globular and elongate galls on characteristics of the galls, and correlation matrix for these variables.

Source of variation		Sum of squares	df	Mean squares	F_s
Corrected total		2599665.20	133		
Adjusted treatment		243.97	1	243.97	.026ns
Regression		1096649.72	4	274162.43	28.86***
Error		1215984.13	128	9499.87	
Regression homogeneity		63056.38	4	1574.10	1.70ns
Error for regression homogeneity		1152927.75	124	9297.80	
Partial regression coefficients				Adjusted treatment means	
GL	GW	LAG	GLL	Globular	Elongate
15.5	26.9	.24	2.3	352.25	356.24
Correlation matrix					
	GL	GW	LAG	GLL	Population Size
GL		.580	-.020	.140	.612
GW			-.164	.313	.676
LAG				.003	-.064
GLL					.240

Note: Treatments are differences between morphs. Gall characteristics used as covariates are: GL—gall length, GW—gall width, GLL—length of leaf bearing the gall, and LAG—number of leaves after the gall position. ***— $P \leq .001$, **— $.001 P \leq .01$, *— $.01 P \leq .05$, ns— $P > .05$. Correlation coefficients significant at $P \leq .01$ are in italics.

morphs, since there was no significant difference between the adjusted treatment means ($F_s = .026 < F_{.05(1,128)}$).

Within tree number 8, the correlation of gall leaf length and population size, for both morphs, was .560 ($n = 20$). However, overall, the correlation of leaf length with population size (.240) and gall dimensions (.140, .313) was low, and within each morph, gall leaf length did not account for the variation in population size. Therefore, it seemed useful to try another variable that might explain gall size and the relationship of gall position to population size in the elongate morph.

Petiole length and width were tried as variables that might affect gall dimensions. Since transverse galls grow on petioles, the size of the latter might be more closely related to gall dimensions than leaf length. For a new pooled collection of 9 globular and 10 elongate galls from a single tree, petiole width explained 78% of the variance in gall width ($F_s = 63.3 > F_{.001(1,18)}$), and petiole length explained 41% of the variance in gall length ($F_s = 12.3 > F_{.005(1,18)}$). Petiole length and width, then, are better indicators of gall dimensions than gall leaf length for transverse galls.

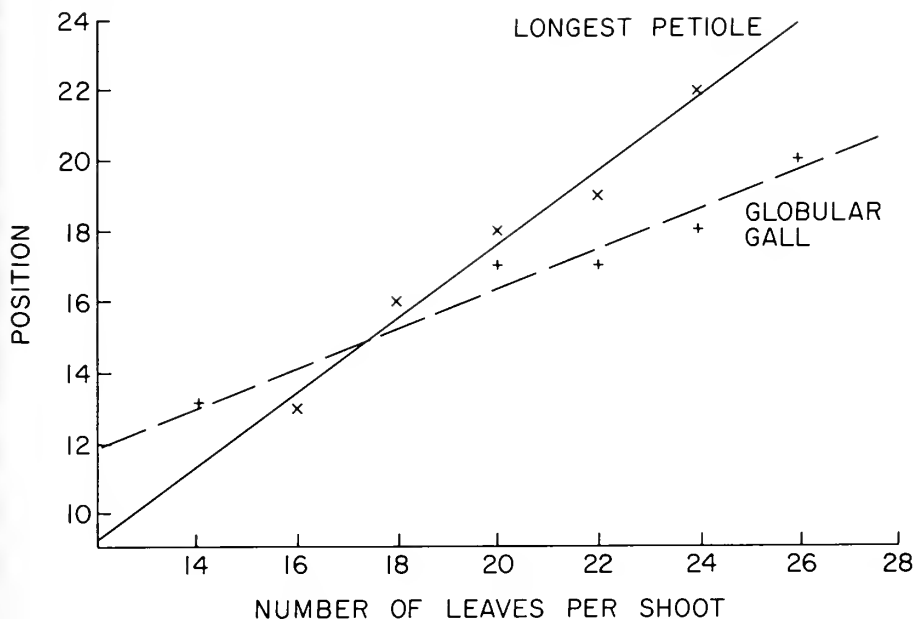


Fig. 1. Position of globular gall (crosses and dashed line) and position of the longest petiole (\times 's and solid line) on the total number of leaves on the shoot. The lines represent significant least squares regression lines. The ordinate is position and the abscissa is total number of leaves. Samples based on tree 2, Stony Brook, New York, 1975. Note that for most shoot sizes the position of globular galls is earlier than that of maximal petiole size.

In this new sample, gall length of the two morphs was not significantly different ($F_s = .5 < F_{.05(1,18)}$), but width of the globular morph was significantly greater than that of the elongate morph ($F_s = 14.7 > F_{.005(1,18)}$). Petiole width for leaves with globular galls was $4.5 \pm .36$ mm and for leaves with elongate galls was $3.1 \pm .22$ mm. My field observations suggest that this difference in width is not due to the presence of the galls on the petioles; measurements of many late and early leaf petioles without galls showed that petiole width of late leaves was rarely as low as 3.0 mm, which was the usual width of early petioles. This difference in petiole width between early and late leaves may indirectly account for the general difference in population size of the two morphs through its effect on gall width. An analysis of covariance was carried out with gall width as the dependent variable, globular and elongate as treatments, and petiole width as a covariate. The regression, controlling for petiole width, was significant ($F_s = 52.4 > F_{.001(2,17)}$). Thus, although petiole width does explain 78% of the variance in gall width for elongate and globular galls taken together, other (possibly genetic) determinants of the differences in gall width of the morphs remain.

In summary, the greater population sizes of globular galls are partly attributable to the greater petiole widths of the late leaves on which these

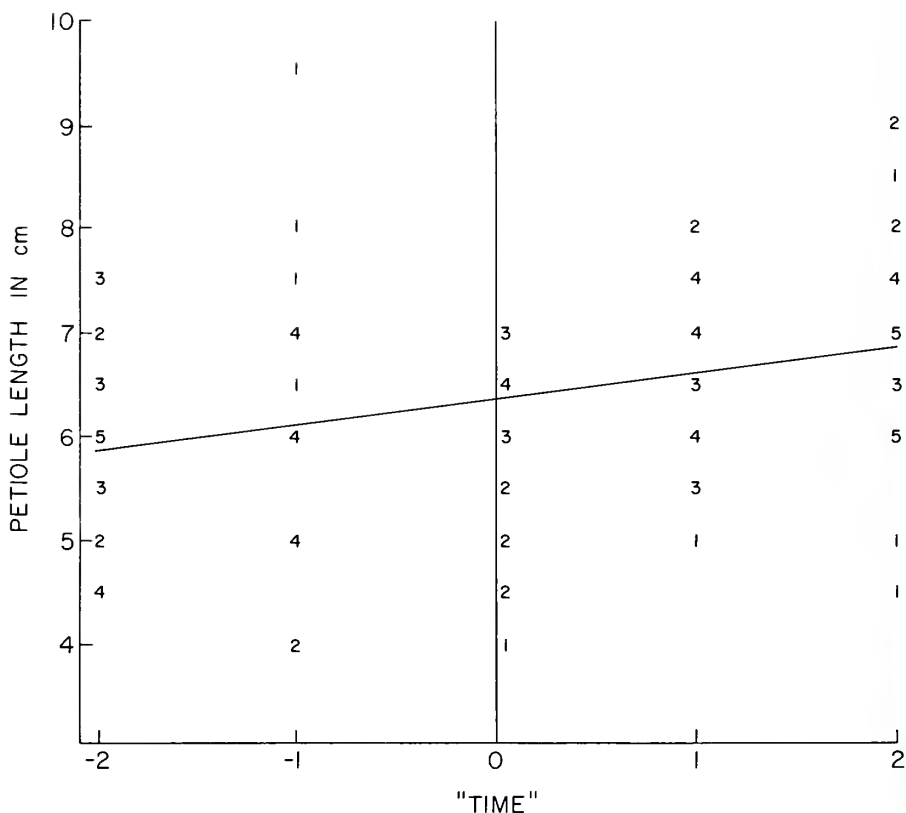


Fig. 2. Regression of petiole length on gall position, holding the total number of leaves constant ($P < .05$). Numbers of graph indicate number of times a given point occurs. The ordinate is petiole length (cm) and the abscissa is "time" (deviation of gall position from regression on total number of leaves per shoot). Sample is made up of globular galls taken from tree 2, Stony Brook, New York, 1975.

galls are found, relative to the petiole widths of the early leaves, which are the sites of the elongate galls.

Position of Globular Galls among the Late Leaves

Position of globular galls, as expected, increases with the total number of leaves on the shoot (Figure 1). Any given time of gall initiation will result in a later position on faster than on slower growing shoots, because the faster shoots will have produced more leaves in the same amount of time. Although population size of a gall did not correlate with gall position, it may correlate with time of gall initiation, which would suggest selective pressure for earlier or later gall initiation. A regression of population size on gall position, controlling for the number of leaves per shoot relates population

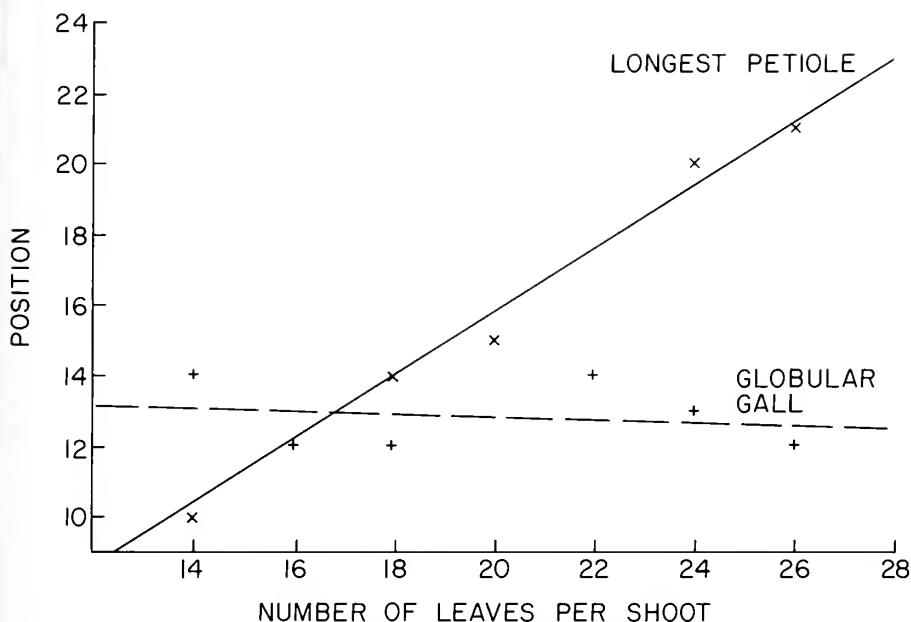


Fig. 3. Globular gall position (+'s and dashed line) and longest petiole position (x's and solid line) on the total number of leaves on the shoot. The solid line represents a significant regression line. Ordinate: position; Abscissa: total number of leaves. Samples are from tree 8, Stony Brook, New York, 1975.

size to time; however, this regression was not significant, so population size is not dependent on time in the data from tree 2.

Since petiole length has been shown to correlate with gall length, I also investigated the possible relationship of position of globular galls with the variation in petiole size of late leaves. Does the position of globular galls maximize petiole size among late leaves? For tree 2, petiole length was regressed on leaf position, holding the total number of leaves constant (Figure 2). Petiole length significantly increased with time, suggesting that later gall initiation may imply an increased population size through the effect of petiole length on gall length. The relationship of the actual positions of globular galls to petiole size is shown in Figure 1. For most shoot sizes, the globular galls appear earlier than the leaf with the longest petiole. The results were similar for another tree (8), as shown in Figure 3. There is no evidence, then, that the globular galls were positioned as an adaption to maximal petiole length among the late leaves.

Positions of Elongate and Oblique Galls among the Early Leaves

For elongate galls alone, petiole length explains 62% of the variation in gall length ($F_s = 17.9 > F_{.001(1,11)}$). Gall leaf length, on the other hand, does

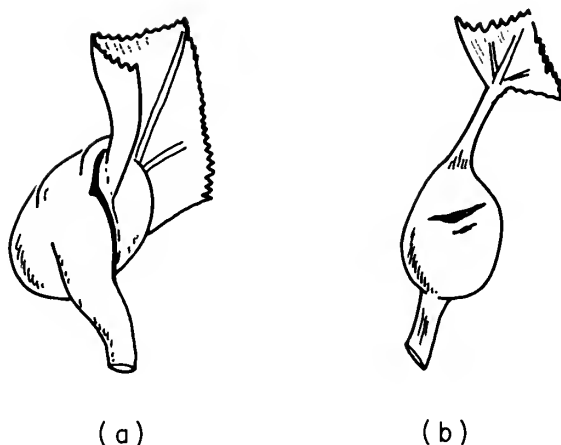


Fig. 4. *Pemphigus* galls. (a) A "typical" gall of *P. populicaulis* ("oblique"). (b) A "typical" gall of *P. populitransversus* ("transverse"). Drawings by Lorenz Rhomberg.

not have a significant correlation with gall length ($r = .156$, $n = 48$). Since gall length was found to correlate highly with population size ($r = .50$, $n = 25$), for tree 4, it might be expected that there would be selection for timing of gall initiation such that the resultant position of the gall provided a larger petiole, on the average. Such selection would be possible if petiole length can be predicted by timing of gall initiation. By contrast, oblique gall diameter correlates more highly with leaf length ($r = .874$, $n = 25$) than with petiole length ($r = .209$, $n = 25$); and gall position might similarly reflect a prediction of leaf size through timing. The reasons for the differences in correlations are clear, since elongate galls are formed on leaf petioles while oblique galls are formed by a twisting together of the base of the leaf blade (Figure 4).

The relative and absolute positions of oblique and elongate galls are not constant from tree to tree (Table 6). Trees 1 and 4 each show elongate galls significantly earlier in position than oblique galls. Tree 3 showed the same trend but the difference was not significant.

Table 6. Mean (\pm standard errors) of oblique and elongate galls of different trees sampled in Stony Brook, New York, 1975.

	Oblique	N	Elongate	N	F_s
Tree number					
1	7.17 \pm .44	15	5.59 \pm .38	22	12.3***
3	8.80 \pm .20	109	8.30 \pm .20	98	3.21ns
4	7.45 \pm .37	21	5.21 \pm .55	19	12.0***
5	6.70 \pm .38	25	—	—	—



Fig. 5. Leaf length as a proportion of maximum length (solid line) and petiole length as a proportion of maximum length (dashed line) on leaf position. Ordinate: proportion of maximum length; Abscissa: leaf position. Data are for tree 1, Stony Brook, New York, 1975.

For a more detailed examination of the shoots on tree 1 we turn to Figure 5. Only shoots without galls having 9, 10, or 11 early leaves were considered to limit the variability of patterns of leaf or petiole size due to variation in the number of early leaves of the shoots. The abscissa gives the leaf position. The ordinate is the ratio of the length for a given position on the shoot to the maximum length for the shoot. The solid line shows the average proportion of maximum leaf length (length divided by the length of the largest leaf on the shoot) and the dashed line shows the average proportion of maximum petiole length for each position on these shoots. The average petiole length at position 6, the first peak, was 7.92, and at position 8, the second peak, was 7.08. Because of the small sample size ($n = 6$) for each group, these differences are only suggestive ($P = .08$). Leaf length follows the reverse pattern with the average at position 8 (12.1), greater than that of position 6 (10.7) ($F_s = 4.25 > F_{.08(1,10)}$). Again this is only suggestive, but it appears that the position with the greatest average petiole length is before the position with the greatest average leaf length for this tree. Another expression of this difference is that for shoots without galls on tree 1, the average position of the longest leaf, 7.6, was significantly greater than the average position of the longest petiole, 6.1 ($F_s = 30.8 > F_{.001(1,30)}$).

Is this difference reflected in the positions of oblique and elongate galls? The frequency distributions of elongate and oblique gall positions for tree

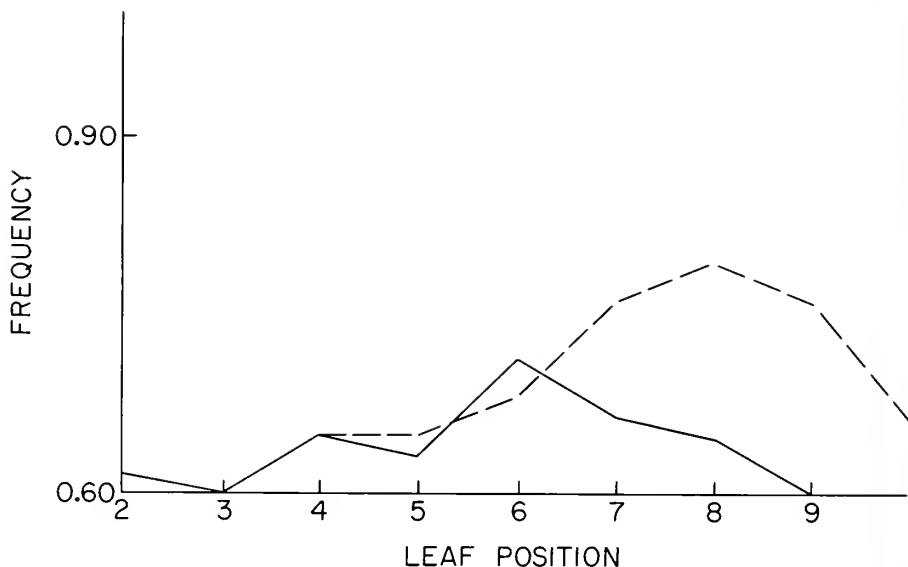


Fig. 6. Frequency polygons of elongate (solid line) and oblique (dashed line) gall positions for tree 1. Ordinate: frequency; Abscissa: leaf position.

1 are shown in Figure 6. The solid line shows the frequency distribution of the position of elongate galls, and the dashed line that of oblique galls. The mean gall positions of the two types differ for these shoots ($F_s = 12.3 > F_{.005(1,47)}$). It is apparent from a comparison of Figures 5 and 6 that both elongate and oblique galls are, on the average, in a position that should result in greater fitness for each. Also, although the figures do not show it, the last 1 or 2 leaves among the early leaves usually have smaller blades and petioles. The oblique and elongate galls, then, are usually on one of the leaf positions that have the greatest average leaf and petiole sizes, respectively.

Similar data are shown for tree 3 in Figures 7 and 8. Here, the positions of oblique and elongate galls are not significantly different (Figure 8). The mean positions are marked as crosses on the lines. The average petiole lengths at the peaks at positions 6 and 8 are also not significantly different ($P = .70$). Elongate and oblique galls again are near the optimal positions, but this time with more overlap between the two species. It may be that the timing of gall initiation of one or both species on tree 3 is slightly different from that of tree 1, but the observed difference in positions is better explained by a greater rate of early leaf expansion in tree 3, creating a higher mean position of each species and at the same time, less separation in position between the two.

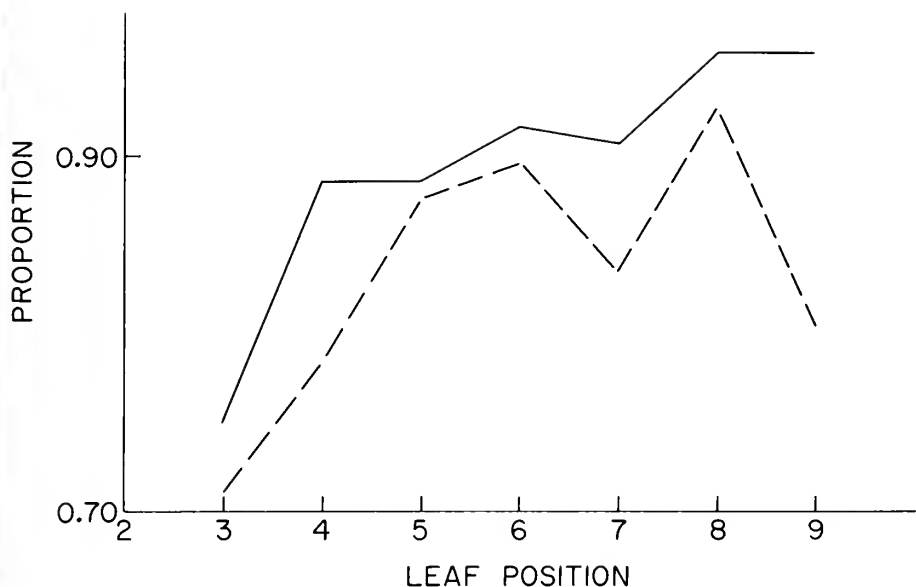


Fig. 7. Average proportion of maximum leaf length (solid line) and petiole length (dashed line) on leaf position. Ordinate: proportion of maximum length; Abscissa: leaf length. Data are for tree 3, Stony Brook, New York, 1975.

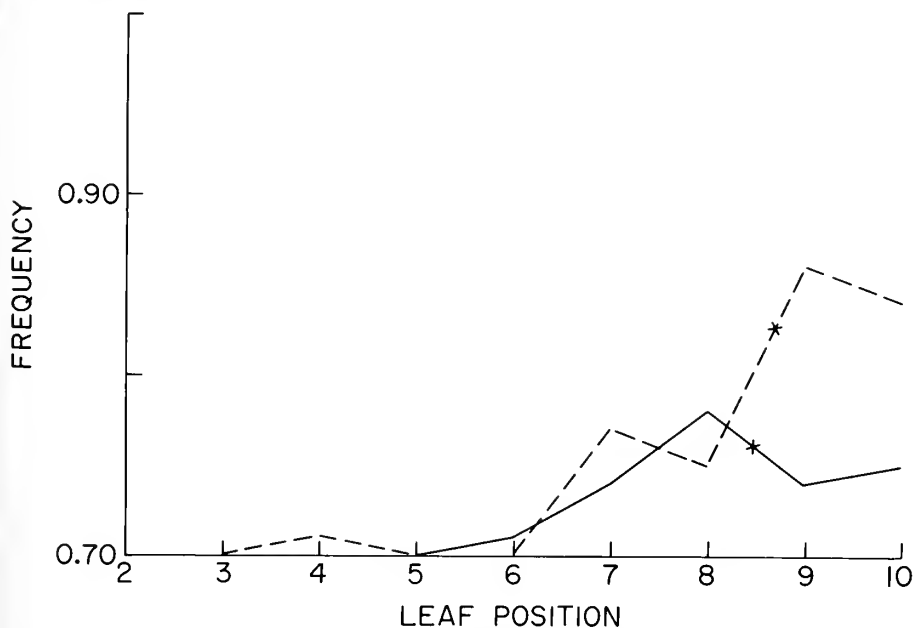


Fig. 8. Frequency polygons of elongate (solid line) and oblique (dashed line) gall positions. Ordinate: frequency; Abscissa: gall positions. Data from tree 3, Stony Brook, New York, 1975.

It appears that the average earlier timing of elongate galls relative to oblique galls may be a strategy to obtain longer petioles, thereby increasing population size. Similarly, oblique gall position seems to correspond to the largest leaf position among the early leaves. If trees had growth patterns similar to that of tree 1, later elongate gall initiation would be selected against. The earlier initiation of elongate galls relative to oblique galls may be a result of the growth pattern in which petiole length, on the average, reaches its peak before leaf length among the early leaves.

Summary

The aphid, *Pemphigus populitransversus*, producing galls on the petioles of cottonwoods, *Populus deltoides*, was shown to comprise two forms differing in time of gall initiation and resulting in galls on early leaves and late leaves of the shoots. This dimorphism in position corresponds to the elongate-globular dimorphism previously described for this species.

The factors determining population size in the galls of these two morphs were explored. In each case, gall length and width correlated strongly with population size. Length of the leaf bearing the gall showed no correlation with population size within each morph. However, leaf length did help account for differences in population size between the two morphs.

The greater population sizes of globular galls are related to their larger size relative to elongate galls. Globular galls were shown to be significantly greater in length, width, and depth measurements. Petiole size was shown to account for much of the variation in gall size in *P. populitransversus*, both among and within morphs. The larger petioles of the late leaves help account for the larger size of the globular galls; hence, the greater population sizes of globular galls is due, in part, to the strategy of late gall formation, through the indirect effect of petiole size on population size.

Within the late leaves, globular galls tended to be formed on leaves before those with maximal petioles. Among the early leaves, elongate galls did seem to be in an average position that matched the position of the longest petiole. The galls of *P. populicaulis* were in a position such that leaf size was nearly maximized. The dimensions of elongate galls were dependent more on petiole size and those of oblique galls more on leaf size. This agrees with their sites of gall formation. The tendency among early leaves for petiole size to reach a maximum before leaf size may explain the slightly earlier initiation of elongate compared to oblique galls.

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EUROPEAN KATYDID *MECONEMA THALASSINUM* (DE GEER)
RECORDED FROM NEW LOCATION ON LONG
ISLAND, NEW YORK (ORTHOPTERA: TETTIGONIDAE)

Burke Smith, Jr.

Abstract.—Establishment of the European katydid *Meconema thalassinum* (De Geer) is confirmed on Long Island, New York. Thirteen specimens taken at Garden City in July 1977, add a third geographic location on Long Island for the species, previously found in much smaller numbers at King's Park (1968) and Little Neck (1957 and 1959). No other North American records are known. Distinguishing morphological characteristics of the species are described and illustrated, and habits (including sound production and food preferences) are discussed.

Thirteen specimens of the European katydid *Meconema thalassinum* (De Geer) were collected by the author at Garden City, Long Island, New York, in July 1977. Known as the Oak Bush Cricket, or Eichenschrecke, this species is widely distributed in Europe (Beier, 1966), but is a rarity in North America, where it has been found previously at only two locations, both on Long Island. It was first recorded at Little Neck, Long Island, where two males and two females were taken in July and August 1957; two other specimens were taken from the same locality in 1959. The specimens from Little Neck were all collected by Mr. John K. Torres, editor of Audubon Magazine, and were reported by A. B. Gurney (1960, 1960a). The next Long Island record was at King's Park, Suffolk County in 1968, where a single male was taken by R. M. Emberson, reported by D. E. Johnstone (1970). The present find establishes a third location for the species on Long Island, with a larger number of specimens taken than heretofore. There are no other North American records known for *Meconema thalassinum*.

When first found on Long Island twenty years ago, Gurney (1960) considered it to be an established adventive, probably introduced from eggs on imported nursery stock. The scarcity of records concerning it since that time (only one specimen being recorded during the seventeen-year interim) would indicate that the species has existed in small localized populations, possibly subject to cyclical variations, or that it may even have died out and been reintroduced. It will be interesting to see what additional records of the species may occur in the future.

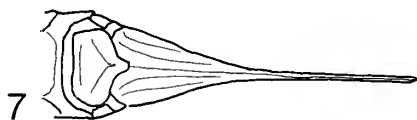
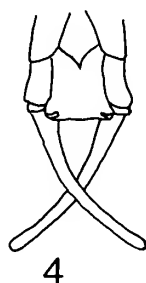
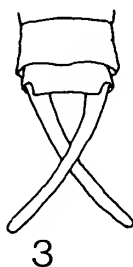
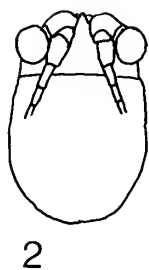
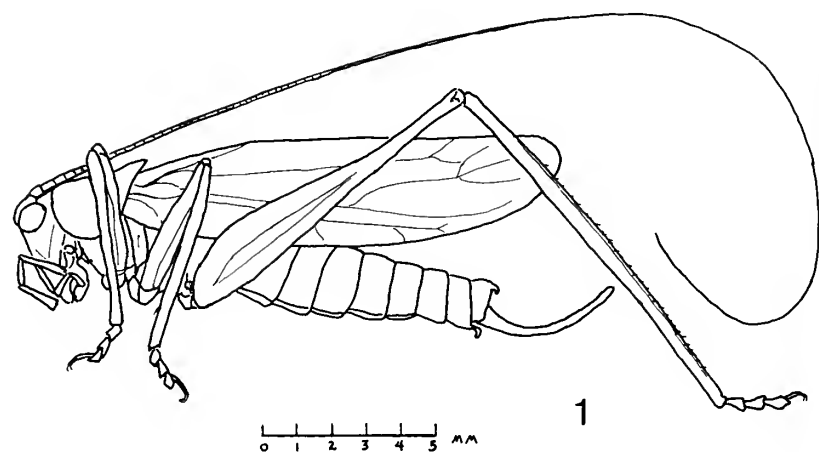
The specimens from Garden City were collected on the porch and grounds of a town-house during the period of July 7 through July 19, 1977. Most were captured in late evening walking around a light on an open porch

ceiling. Several specimens were taken when they were at rest on the porch ceiling during the day. In all, ten males and three females were collected; Dr. Irving J. Cantrall, University of Michigan Museum of Zoology, identified the species as *Meconema thalassinum* (De Geer). Specimens have been deposited in the University of Michigan Museum of Zoology, the Field Museum of Natural History, and the Academy of Natural Sciences, Philadelphia.

Meconema thalassinum is a rather small katydid, of the subfamily Meconematinae, having a body length of 11–15 mm, with tegmina extending about 3–4 mm beyond the apex of the abdomen (Fig. 1), and is thus not likely to be confused with the larger and more robust North American katydids of the subfamilies Phaneropterinae and Pseudophyllinae. Gurney (1960) has pointed out that the species does superficially resemble some of the native meadow grasshoppers of the subfamily Conocephalinae (genera *Orchelimum* and *Conocephalus*) which however have the tympana of the fore-tibia covered, except for a slit-like opening, whereas the tympana of *Meconema thalassinum* are exposed (Fig. 5). Also, in *Meconema thalassinum*, the tegmina of males and females closely resemble each other and are without any special sound-producing organs. *Meconema thalassinum* may also be distinguished by special structural characteristics of the genital areas as shown in Figs. 3, 4, 6, and 7. The male cerci are about 4 mm long, strongly curved, without the lateral projections found in native North American katydids, and with the apices scarcely specialized; the male sub-genital plate is short, apically truncate and bears two small moveable lateral appendages; the ovipositor is about 9 mm long, slightly curved and pointed, and without serrations.

The habits of this species in Europe, as described below, have been well described in handbooks by various authors, including Chopard (1951), Harz (1957) and Ragge (1965). Gurney (1960) and Johnstone (1970) have also summarized and commented on observations made by previous investigators.

Meconema thalassinum is part of the Palaearctic arboreal fauna in Europe, occurring on oaks and other deciduous trees, as well as on pines. It may be found intermittently in parks, gardens and tree-rows in urban areas, especially where there are large, old trees. The location in Garden City, Long Island, provides such a habitat with its large well-established maple trees. The species is nocturnal, individual insects remaining quiet during the day and becoming active at twilight. Perhaps the scarcity of records on Long Island may be due in part to these habits. Although some authors (Chopard, 1951; Ragge, 1965) have stressed its carnivorous habits, the species appears to be essentially omnivorous (Johnstone, 1970), feeding on oak and other deciduous leaves as well as on a variety of insects.



Figs. 1-7. *Meconema thalassinum* (De Geer). 1. Male, lateral view. 2. Head, dorsal view, showing shape of fastigium. 3. Dorsal view of supra-anal plate and cerci of male. 4. Ventral view of sub-genital plate and cerci of male. 5. Front leg, showing open tympanum. 6. Lateral view of ovipositor. 7. Ventral view of ovipositor, showing sub-genital plate of female.

The males lack the stridulatory apparatus which is found almost universally in other Tettigoniidae, but nonetheless make a "purring" or "drumming" sound. There have been conflicting reports on how this sound is produced. Some investigators (Currie, 1953; Harz, 1955) have indicated that it is caused by the rapid beating of a body part (probably a hind leg) on the substratum. However, Cappe de Baillon (1921) suggested that in connection with the rapid body movements associated with sound production, the tegmina, which are held above the body, may be rubbed together to produce the actual sound. There are microscopic teeth on the dorsal distal portion of the tegmina which could be used in sound production, but there have been no confirming observations that this is actually the case. Further observations are obviously needed in this respect.

In Europe eggs hatch in May, with adults being found from July through October. Females come down from the tree-tops to lay eggs in the cracks of rough-barked trees, or in lichens covering the tree trunks, from the beginning of September until the last of October. Whether the species has modified any of its behavior patterns or life span on Long Island, remains to be determined.

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A NEW SPECIES OF *MEGARIS* AND THE STATUS OF THE
MEGARIDIDAE MCATEE & MALLOCH AND
CANOPIDAE AMYOT & SERVILLE
(HEMIPTERA: PENTATOMOIDEA)

F. J. D. McDonald

Abstract.—A new species of *Megar*is is described. Descriptions are given of the male genitalia of *Megar*is *stalii*, *M. constricta*, *Canopus caesus*, *C. orbicularis* and *C. impressus*. The spermatheca and external female genitalia are described for *Megar*is *laevicollis*, *M. atratula*, *Canopus burmeisteri*, *C. impressus*, *C. fabricii*, *C. caesus* and *C. orbicularis*. From a consideration of all available morphological evidence the family status of Megarididae and Canopidae is confirmed. Neither family is closely related to the Plataspidae.

Very little work has been done on the interesting and unusual insects of the genera *Canop*is Fabricius and *Megar*is Stål since McAtee and Malloch's revision in 1928. Barber (1939) added *Megar*is *puertoricensis* and Kormilev (1956) described *Megar*is *vianai*. Another species is added in this paper.

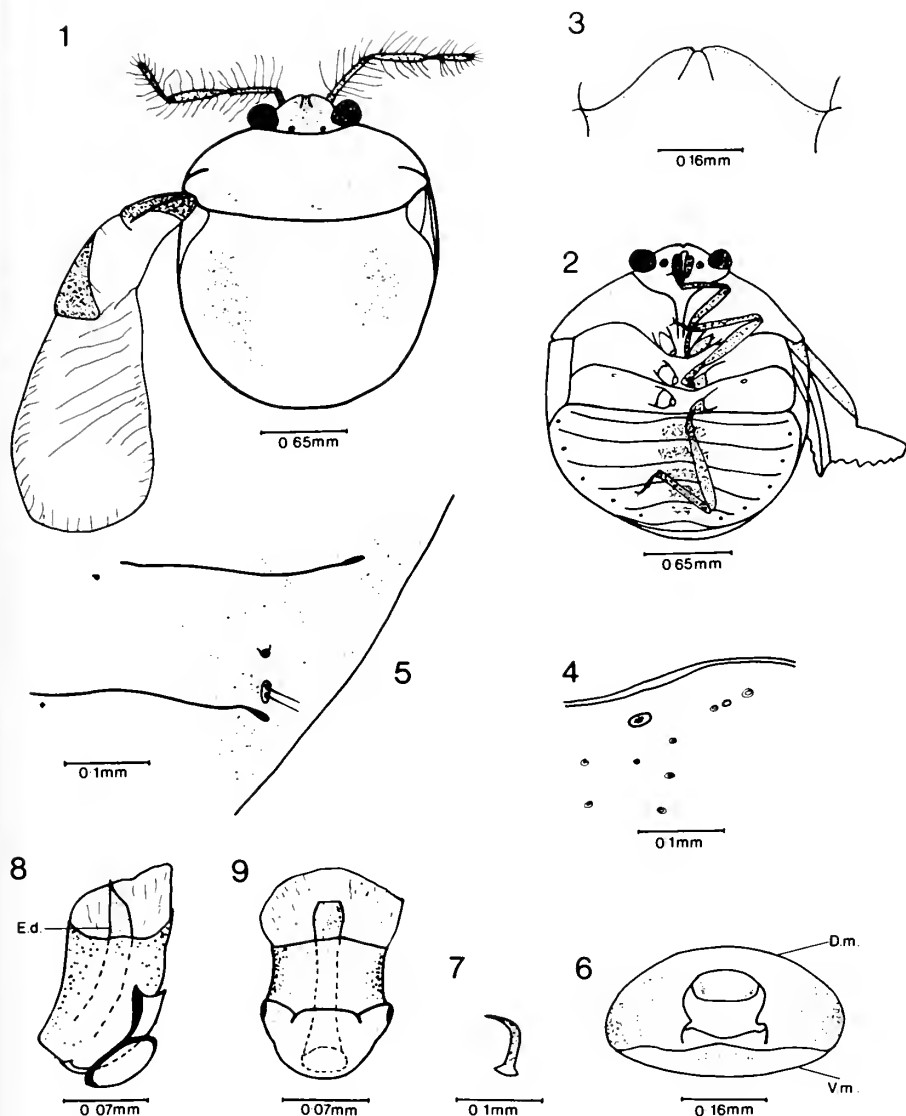
The general characteristics of these two genera have been very clearly set out in McAtee and Malloch's (1928) paper. I have attempted in this paper to examine these genera in more detail and come to some conclusion as to their correct status within the Pentatomoidea. The two genera were put in separate subfamilies within the family Pentatomidae by McAtee and Malloch. However the Pentatomidae of these authors is equivalent to the Pentatomoidea in most current classifications. Descriptions of the pygophore and external female genitalia are given to facilitate species recognition.

*Megar*is *rotunda* n. sp.
(Figs. 1-9)

Typical small oval megaridid (Fig. 1) with the scutellum completely covering the dorsal surface of the abdomen. Ventral surface flat (Fig. 2), dorsal surface steeply convex. Head tucked into the prothorax and protruding but little beyond it. Shiny rich reddish brown all over.

Head.—Head broader than long, eyes prominent, globular. Jugae (Fig. 3) short, converging, not completely meeting at apex of tylus. Antennae four segmented; all segments provided with very long fine setae; first segment short, second longest, third and fourth subequal.

Bucculae very short, indistinct. First rostral segment extending beyond bucculae by almost a half its length; rostrum not exceeding hind coxae.



Figs. 1-9. *Megaris rotunda* n. sp. 1. Dorsal view. 2. Ventral view. 3. Apex of head, dorsal view. 4. Stink gland aperture. 5. 5th abdominal sternite. 6. Pygophore. 7. Right clasper. 8. Aedeagus, lateral view. 9. Aedeagus, dorsal view. Dorsal margin (D.m.), endophthallic duct (E.d.), ventral margin (V.m.).

Thorax.—Pronotum steeply declivous anteriorly, lateral angles with a rounded protuberance. Mesoscutellum covering abdomen entirely excepting corium where exposed by incision in anterolateral margins of mesoscutellum. Hemelytron (Fig. 1) heavily sclerotized along anterior half of margin, this portion terminating in large triangular red callus; remainder membranous, smoky brown. Membrane with a number of faint cross veins. Posterior wing membranous with a number of sclerotized veins. Hemelytron folded under scutellum; fold occurs at junction of callus and membrane.

Propleura raised anteriorly into collar, deeply grooved by sternum. Meso- and metapleura flat and plate-like. Metathoracic stink gland (Fig. 4) orifice minute, represented by an oval raised area; no evaporative area developed.

Coxae small, flattened, lying close to sterna; trochanters about same size as coxae, fused to the femora. Femora elongate, swollen medianly. Tibiae shorter than femora, uniform in diameter, provided with numerous fine short setae. Tarsi two segmented; first segment half the length of the second, latter bearing a pair of claws and pulvilli; both segments with a number of short fine setae.

Abdomen.—Sterna bowed cephalad medianly; sutures delimiting each segment terminating before reaching lateral margin. Spiracles near lateral margins of segments 2–7; trichobothria paired (Fig. 5), placed one behind other, very slightly laterad of spiracles.

Male genitalia.—(Figs. 6–9.) Pygophore opening facing caudad (Fig. 6), dorsal and ventral margin flattened into a broad rim surrounding the opening. Proctiger small, box-like. Claspers (Fig. 7) minute, L-shaped, apically acute.

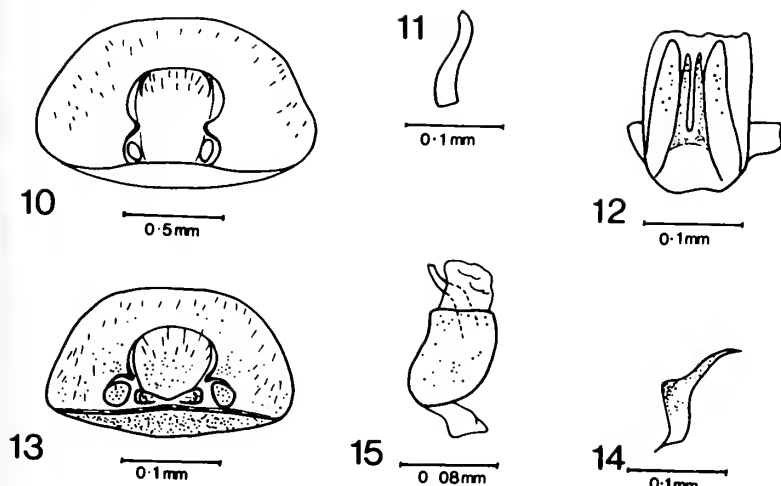
Aedeagus (Figs. 8, 9.) Basal plates large in relation to theca, latter squat, cylindrical, lightly sclerotized. Conjunctival appendages not apparent, membranous sheath surrounding apex of endophallic duct; latter short and tubular.

Female genitalia—not seen.

Diagnostic measurements:

Length		2.18 mm
Breadth		1.87 mm
Width between eyes		0.37 mm
Rostrum		1.15 mm
Antennal segment	I	0.22 mm
	II	0.50 mm
	III	0.44 mm
	IV	0.43 mm

Type.—Holotype, male, labeled: Brasilien, Nova Teutonia, 27°11'N 52°



Figs. 10–12. *Megarís stali*. 10. Pygophore. 11. Right clasper. 12. Aedeagus, dorsal view.

Figs. 13–15. *Megarís constricta*. 13. Pygophore. 14. Right clasper. 15. Aedeagus, lateral view.

23°L, 300,500 m. 11.1.1973. Fritz Plauman. (Deposited United States National Museum.)

Description of the Genitalia of Some Species of *Megarís* and *Canopus*

Male genitalia.

Megarís stali McAtee and Malloch (Figs. 10–12). Pygophore (Fig. 10). Opening dorsal, surrounded by wide flattened area. Ventral border slightly sinuous with a vertical outer face forming caudal face of pygophore. Dorsal border bearing spine-like protuberances on each side above claspers; central border broadly arched, partially enclosing base of box-like proctiger. Claspers (Fig. 11), minute, conical, flattened, lying in rounded recess at each side beneath the ventral border.

Aedeagus (Fig. 12). Theca small, tubular, lightly sclerotized. One pair of strap-like conjunctival appendages. Ejaculatory duct straight, tubular, retracted wholly within theca when at rest, moderately sclerotized.

Megarís constricta McAtee and Malloch (Figs. 13–15). Pygophore (Fig. 13). Opening facing dorsad, surrounded by wide flange, mainly concealed beneath scutellum; ventral face vertical and heavily sclerotized. Dorsal margin deeply emarginate centrally, bearing small projections on each side.

Ventral margin straight. Proctiger tubular, lightly sclerotized, bearing a number of stout setae on dorsal surface. Claspers (Fig. 14) very small with a stout stem, apically tapering to a slender curved process.

Aedeagus (Fig. 15). Theca small cylindrical. One pair of membranous conjunctival appendages (not expanded). Endophallic duct small tubular and slightly sinuous, moderately sclerotized.

Canopus caesus (Germar) (Figs. 16–19). Pygophore (Fig. 16). Opening facing dorsad, ventral face of pygophore vertical. Ventral border straight; internally lying below the border is a thin arched shelf attached mesally and projecting caudad so that apex of arch is in line with ventral border. Dorsal border omega-shaped, merging lateroventrally with ventral border. Claspers (Fig. 17), lying on each side of ventral shelf, L-shaped; apical arm rod-like, bearing near apex on outer margin a long slender curved process. Medianly clasper expanded and flattened, bearing a number of long setae; basal stem narrow flattened.

Aedeagus (Figs. 18, 19). Theca small, squat, heavily sclerotized except for a band around apical margin and basally. One pair of strap-like membranous conjunctival appendages, basally with a small lobe. Median penial lobes fused, membranous except for outer margin which is heavily sclerotized, basally surrounding ejaculatory duct; latter thick, cylindrical, heavily sclerotized, bearing on dorsal surface a small elongate apically acute process.

Canopus orbicularis Horvath (Figs. 20–22). Pygophore (Fig. 20). Opening facing dorsad; ventral border straight; internally ventral wall of pygophore bearing an oblong plate attached midway at its base; plate projects freely upwards, bowed. Dorsal border omega shaped, surrounding base of proctiger centrally; latter box-like. Claspers (Fig. 21), L-shaped; apical arm flattened, blade-like, bearing near apex on outer margin a long thin curved process; mid portion of clasper expanded and somewhat flattened, bearing a number of long fine setae; stem of clasper cylindrical.

Aedeagus (Fig. 22). Theca squat, heavily sclerotized except for apical rim. One pair of membranous strap-like conjunctival appendages, apically bifid with two short rounded lobes. Median penial lobes fused into trough-like structure beneath vesica; ventral surface well sclerotized, dorsal surface

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Figs. 16–19. *Canopus caesus*. 16. Pygophore. 17. Right clasper. 18. Aedeagus, lateral view. 19. Aedeagus, ventral view.

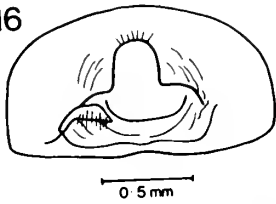
Figs. 20–22. *Canopus orbicularis*. 20. Pygophore. 21. Right clasper, lateral view. 22. Aedeagus, lateral view.

Figs. 23–26. *Canopus impressus*. 23. Pygophore. 24. Right clasper, lateral view. 25. Aedeagus, lateral view. 26. Aedeagus, ventral view. Conjunctival appendage (C.a.), sclerotized process (S.p.).

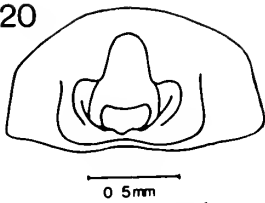
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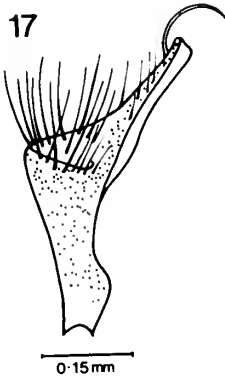
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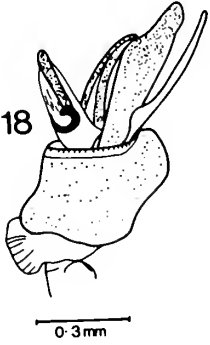
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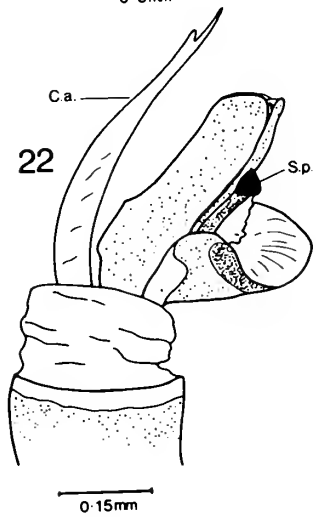
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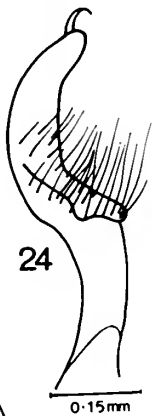
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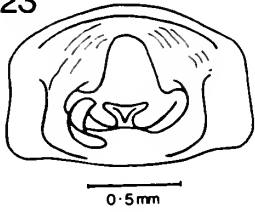
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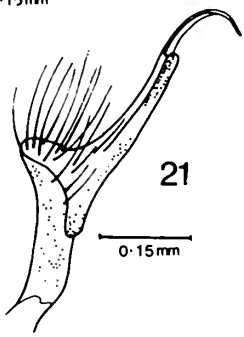
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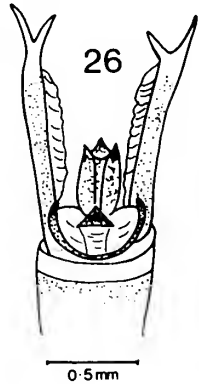
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membraneous. Endophallic duct large, tubular, heavily sclerotized, bearing on ventral surface a heavily sclerotized process, apically triangular, tapering basally.

Canopus impressus (Fabricius) (Figs. 23–26). Pygophore (Fig. 23). Ventral border straight, medianly somewhat thicker than in *C. orbicularis*, internally bearing a stalked oval plate-like projection somewhat similar to one found in *C. orbicularis*. Dorsal border with deep median V-shaped incision, laterally merging with ventral border; proctiger oblong, flattened, enclosed partially in median incision in dorsal border. Claspers (Fig. 24), shallow hook-shaped; anterior arm cylindrical apically, broadly rounded, bearing small curved process near apex on outer margin; clasper flattened medianly, bearing a number of long fine setae; stem cylindrical, tapering basally.

Aedeagus (Figs. 25, 26). Theca squat, cylindrical, bearing oblong shield-like extension on ventral margin; lateral and ventral apical margins unsclerotized. One pair of flattened blade-like conjunctival appendages sclerotized except for apices, latter bifid, produced into two short rounded arms. Median penial lobes fused into sclerotized trough-like structure lying below endophallic duct, latter large, tubular, sclerotized, bearing elongate process on ventral margin.

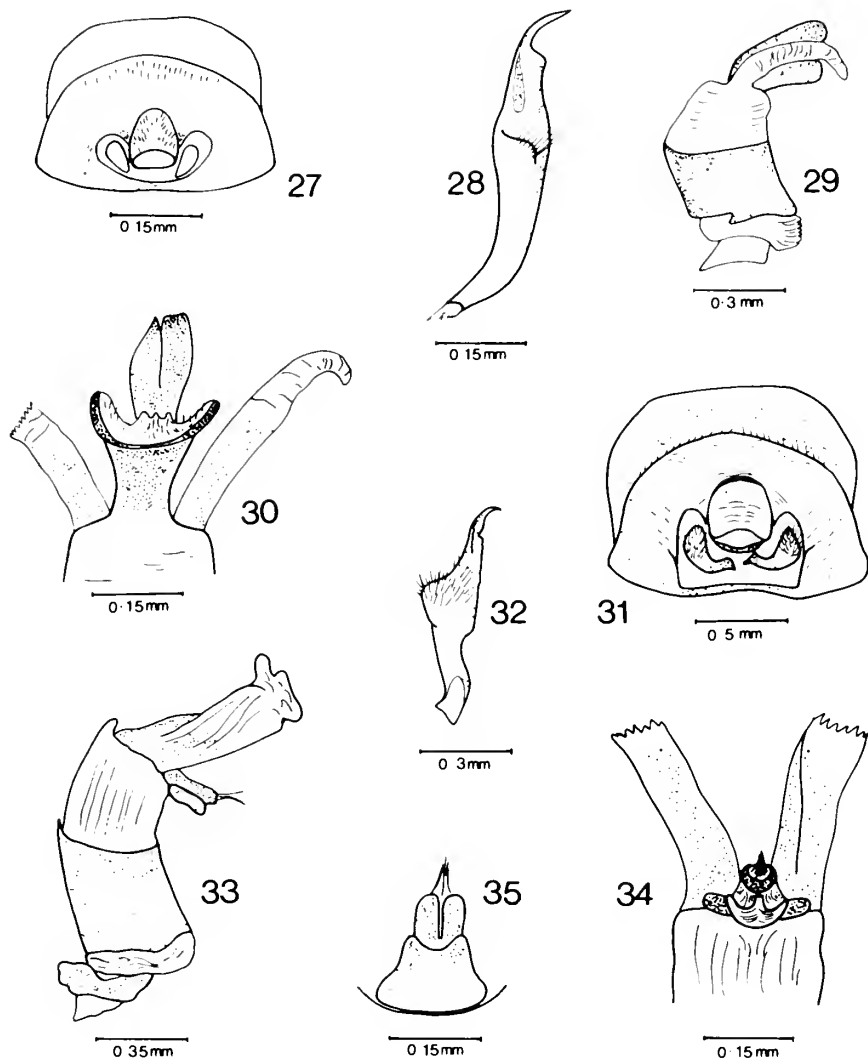
Notes.—These three species are very similar showing a distinct gradation in characters. The process on the clasper is smallest in *C. impressus* and longest in *C. caesus* and *C. orbicularis*. The plate lying beneath the ventral margin varies in shape in the three species being almost free in *C. impressus* and more elongate in *C. caesus*. The aedeagus also is very similar in the three species.

Canopus burmeisteri McAtee and Malloch (Figs. 27–30). Pygophore (Fig. 27). Opening surrounded by wide flat flange, dorsal border smoothly arched, ventral border straight. Proctiger small, tubular. Claspers (Fig. 28) elongate rod-like, apically tapering into a long thin curved process, a number of long setae found mid-laterally.

Aedeagus (Figs. 29, 30). Theca small, tubular, bearing large ring-like collar when expanded out, normally recessed within theca. One pair of elongate tubular conjunctival appendages, feebly sclerotized basally, apically membraneous. Median penial lobes fused into sclerotized trough-like structure lying beneath the endophallic duct; latter stout, oblong, heavily sclerotized.

Canopus germari McAtee and Malloch (Figs. 31–35). Pygophore (Fig. 31). Opening surrounded by wide flat flange, ventral margin straight, dorsal margin arched with two sharp V-shaped projections on either side of base of proctiger. Latter small, tubular. Claspers (Fig. 32) broad centrally, bearing a number of long setae, apically tapering and drawn into a fine hook; basally clasper with a tubular stem.

Aedeagus (Figs. 33–35). Theca small, squat, cylindrical, bearing mem-



Figs. 27–30. *Canopus burmeisteri*. 27. Pygophore. 28. Right clasper, lateral view. 29. Aedeagus, lateral view. 30. Aedeagus, ventral view.

Figs. 31–35. *Canopus germari*. 31. Pygophore. 32. Right clasper, lateral inner view. 33. Aedeagus, lateral view. 34. Aedeagus, ventro-apical view. 35. Median penial lobes.

braneous collar apically, invaginated within theca when at rest. One pair of flat oblong conjunctival appendages (probably tubular when fully expanded), apically membraneous, sclerotized towards base. Median penial lobes fused into a pyriform body (viewed ventrally), lying beneath the apex of the en-

dophallic duct; margins of lobes curved inwards forming a trough-like structure on the dorsal surface. Endophallic duct tubular, slightly sinuous, moderately sclerotized, apex diffuse, the whole structure lying in the trough formed by median penial lobes.

Canopus fabricii McAtee and Malloch (Figs. 36–38). Pygophore similar to *C. burmeisteri*, ventral margin slightly thickened. Claspers (Fig. 36), very similar to *C. burmeisteri*, with a large number of setae and somewhat stouter centrally.

Aedeagus (Figs. 37, 38). Theca squat, cylindrical, bearing apical sheath normally retracted within theca. One pair of conjunctival appendages, each bifid, one short arm and one longer tapering arm, longer arm membranous slightly sclerotized basally. Median penial lobes fused into a boat-like structure lying below the endophallic duct; latter stout, sinuous.

Notes. This species differs from *C. burmeisteri* in the following regards. Conjunctival appendages bifid, single in *burmeisteri*; median penial lobe smaller and differing in shape, *burmeisteri* more trough-like; ejaculatory duct slender, thicker and stouter in *burmeisteri*.

Female genitalia.

Megaritis laevicollis Stål (Figs. 39, 40). Spermatheca (Fig. 39) simple globular structure surrounded by a larger membranous sac. No sclerites present around spermathecal opening.

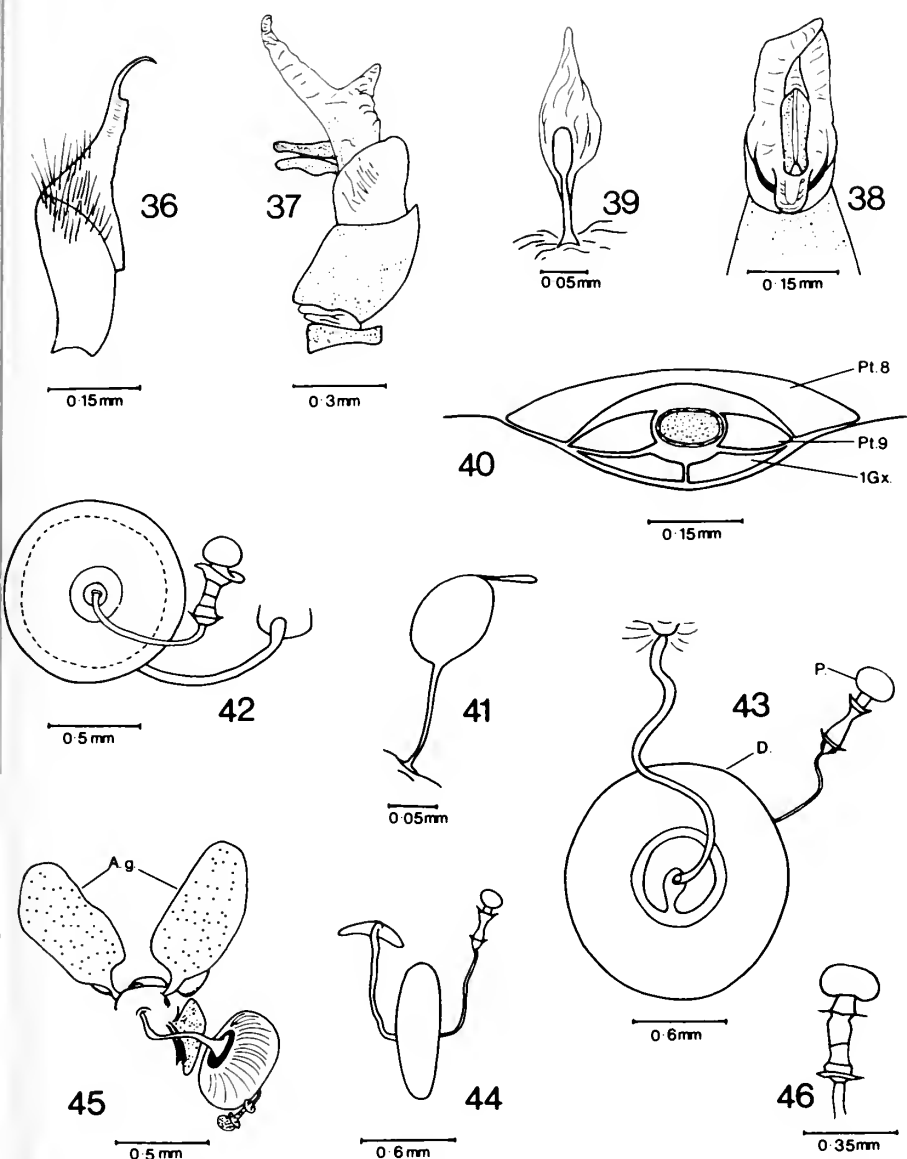
External genitalia (Fig. 40). Paratergites 8 fused centrally by narrow median band. Paratergites 9 lying one on either side of oval tenth segment, each paratergite concave centrally and fitting around tenth segment. First gonocoxae large, plate-like, mostly hidden under abdominal sterna; apical margins of each gonocoxa turned upwards forming all that is visible externally, which consists of a small oblong plate tapering to a fine point laterad.

Megaritis atratula Stål (Fig. 41). Spermatheca a simple bulb with a small elongate appendix apically. No sclerites surrounding spermathecal opening.

External genitalia (Fig. 40) similar to *M. laevicollis*.

Canopus burmeisteri McAtee and Malloch (Fig. 42). Spermatheca (Fig. 41) consisting of well developed pump with proximal and distal flanges connected to sclerotized wheel-like spermathecal dilation. Duct from pump enters one side of spermathecal dilation centrally and a duct exits from other side centrally connecting spermatheca to vulva. Spermathecal dilation provided with a number of internal circular canals. Entrance of spermatheca into vulva without surrounding sclerites. Large paired sac-like accessory glands found ventrally, one on each side of spermathecal entrance. Vulva provided with paired interlocking sclerotized rami.

External genitalia described by McAtee and Malloch.



Figs. 36–38. *Canopus fabricii*. 36. Right clasper, inner view. 37. Aedeagus, lateral view. 38. Aedeagus, ventral view.

Figs. 39–40. *Megaritis laevicollis*. 39. Spermatheca. 40. Female genitalia.

Fig. 41. *Megaritis atratula*. Spermatheca.

Fig. 42. *Canopus burmeisteri*. Spermatheca.

Fig. 43. *Canopus impressus*. Spermatheca.

Fig. 44. *Canopus orbicularis*. Spermatheca.

Figs. 45–46. *Canopus fabricii*. 45. Spermatheca and accessory glands. 46. Spermathecal bulb. Accessory glands (A.g.), spermathecal dilation (D.), first gonocoxite (1 Gx), pump (P.), paratergite 8 (Pt. 8), paratergite 9 (Pt. 9).

Canopus impressus Fabricius (Figs. 43, 44). Similar to *C. burmeisteri*, interlocking rami and accessory glands present.

Canopus fabricii McAtee and Malloch (Figs. 45, 46). Similar to *C. burmeisteri*. Accessory glands (Fig. 45) large, covered with minute spines. Spermathecal dilation with internal striations. Interlocking rami present.

Canopus orbicularis Horvath. Similar to *C. burmeisteri*. Duct between spermathecal opening and dilation longer and more coiled than in *C. burmeisteri*. Interlocking rami and accessory glands present.

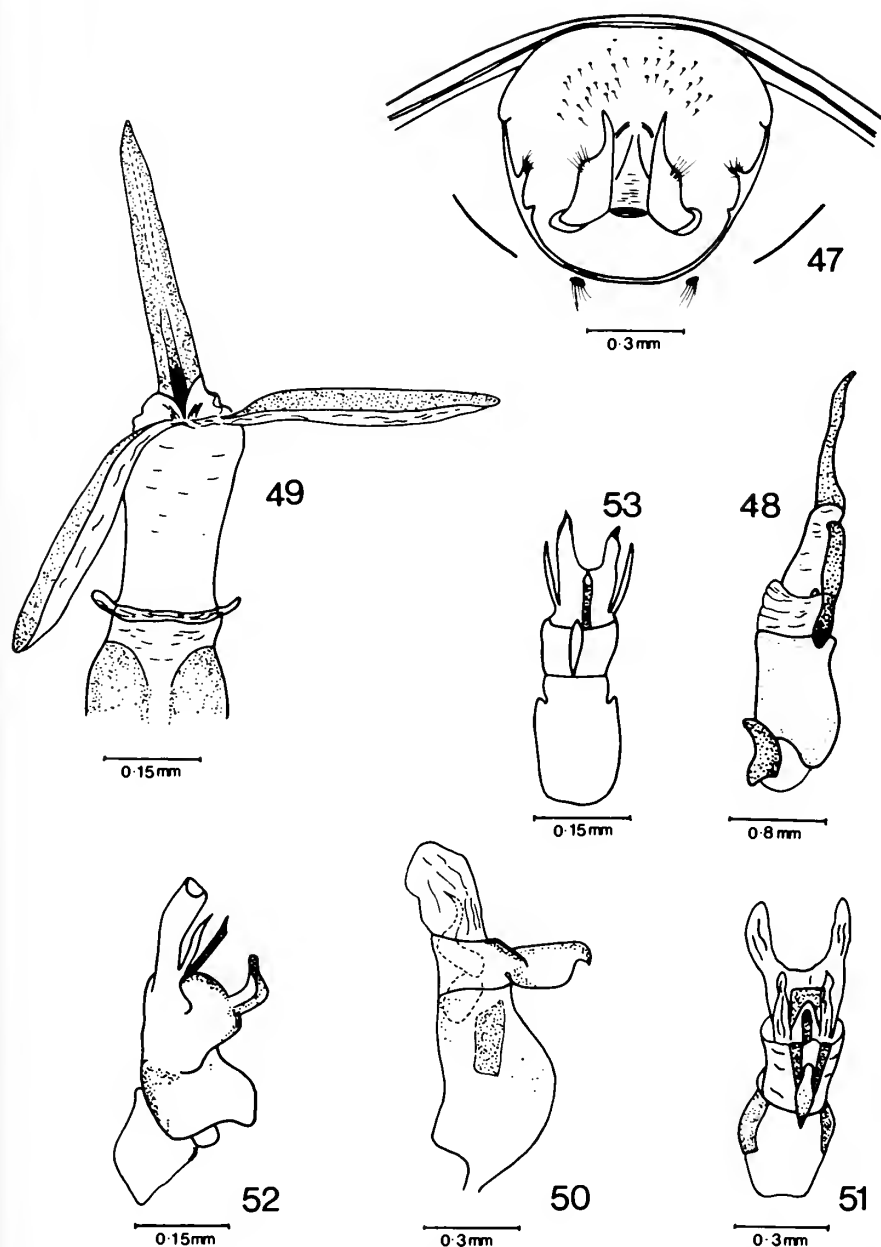
Discussion

It is clear from an examination of the male and female genitalia and of other characters cited by McAtee and Malloch (1928) that the genera *Megaridius* and *Canopus* each warrant family status.

The Canopidae have a well developed series of parallel veins in the forewing whereas the Megarididae have no veins or only one major vein in the membrane. The male genitalia of the three megaridids examined are very simple, consisting of an unsclerotized conjunctiva surrounding a tube-like endophallic duct. The female spermatheca in two species examined is also simple and sac-like without a complicated pumping mechanism. The canopids examined all show much more highly evolved male and female genitalia. The male genitalia have well defined conjunctival appendages together with conjunctival processes associated with the endophallic duct. The females have a complex spermatheca with a well developed circular dilation or reservoir together with a well developed pumping mechanism. The vulva has paired interlocking rami on each side resembling those found in some species of Scutelleridae, and paired accessory glands were also found resembling some species of Cydnidae (McDonald, 1966).

Preliminary examination of the male and female genitalia of some species of Australian Plataspidae indicates that neither the canopids nor megaridids are closely related to this family (McAtee and Malloch, 1928). In the structure of the wing venation, however, the Canopidae do show some affinity with the Plataspidae in possessing parallel venation in the membrane. The spermatheca in the plataspids (McDonald, 1970) has a well developed pump but no dilation or reservoir in the duct. The males have a well developed aedeagus (Figs. 47-53) with conjunctival appendages, but these do not resemble the type of aedeagus found in either the Megarididae or Canopidae. The abdominal sutures in the nymphs (McAtee and Malloch, 1928) also distinguish these two families from the Plataspidae.

From the information so far obtained it would appear that the Megarididae, Canopidae and Plataspidae, while superficially resembling one another in possessing a well developed scutellum, are quite clearly separate families



Figs. 47-49. *Brachyplatys flavipes*. 47. Pygophore. 48. Aedeagus, lateral view. 49. Aedeagus, ventral view.

Figs. 50-51. *Coptosoma falloui*. 50. Vesica, lateral view. 51. Vesica, dorsal view.

Figs. 52-53. *Coptosoma hemispherica*. 52. Vesica, lateral view. 53. Vesica, dorsal view.

and are not closely related. The Megarididae are very primitive and are probably an early offshoot from the Pentatomoid line of evolution. The Canopidae are more highly evolved and show some affinity to the Scutelleridae. The Plataspidae have some affinity with the Pentatomidae but are not closely allied to them.

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AUTOGRAPHA CALIFORNICA NUCLEAR POLYHEDROSIS
VIRUS (NPV) IN A VERTEBRATE CELL LINE:
LOCALIZATION BY ELECTRON MICROSCOPY

Arthur H. McIntosh, Karl Maramorosch and Russell Riscoe

Abstract.—The nuclear polyhedrosis virus (NPV) of *Autographa californica* has been localized by electron microscopy in the cytoplasm of poikilothermic vertebrate cells (VSW). C-type particles carried by this cell line were also visualized together with baculovirus particles in a vacuole-like organelle. Inoculation of VSW cells with *A. californica* NPV had a retarding effect on cell growth.

Nuclear polyhedrosis viruses (NPVs) are the agents of choice for the control of agricultural and forests pests (WHO 1973). Their selection is based on their specificity for insect hosts and their apparent innocuous nature for higher animals (Heimpel 1966; Heimpel and Buchanan, 1967; Ignoffo and Heimpel 1965). However, it is important that both *in vivo* and *in vitro* systems become available for the evaluation of such agents prior to widespread use in the field. There have been no reports concerning the successful replication of NPVs in vertebrate cells other than that of Himeno et al. 1967. Amongst the theories purported to explain this is that virus does not penetrate vertebrate cells. In the present report we tested this premise. A vertebrate viper cell line (VSW) known to replicate an insect Chilo iridescent virus (McIntosh and Kimura, 1974) was inoculated with *A. californica* AC NPV (Vail et al. 1970) at a multiplicity of infection of 1.5 (TCID₅₀/cell). Cultures were incubated at 28°C for 5 days, then prepared for electron microscopy as described previously (McIntosh and Kimura 1974).

The results of the electron microscopy study are present in Figs. 1 and 2. NPV particles (arrows) can be readily seen intracellularly amongst the C-type particles which are carried by this line (Fig. 1). In Fig. 2 a NPV particle with envelope partially removed can be seen extracellularly with many C-type virions. No increase in virus titer could be observed over the 5-day incubation period and this confirms our previous finding (McIntosh and Shamy 1975). However, it was observed that many more C-type particles were present in inoculated cultures than in unchallenged cultures. Since C-type particles do not produce a cytopathic effect, it is not possible to titrate them until such a system is made available. Particle counting using the electron microscope would be an alternative means of quantitating them.

An interesting result was the marked retardation in cellular growth following challenge with AC NPV. At the end of 1 week incubation cell counts



Fig. 1. Intracellular localization of *A. californica* NPV particles (arrows) in a vertebrate VSW cell. Note the presence of C-type particles. $\times 60,000$.

were twice as high in control cultures as in inoculated cultures. When subcultures were made by making a 1:2 split the subculture from the inoculated VSW did not grow out and the pH became very alkaline. Control VSW cells challenged with extracts of the insect cell line TN-368 (Hink 1970) in which AC NPV is propagated, grew normally.

The present findings show that AC NPV is incorporated intracellularly into the vertebrate VSW cell line. The means by which such incorporation occurs are unknown. It is also apparent that intracellular localization of virus particles has a retarding effect on cell growth. It thus appears that failure of AC NPV to replicate in the VSW cell line is not due to lack of uptake by the cells.

Acknowledgments

This investigation was supported in part by a National Science Foundation grant BMS 74-13608, a Rockefeller Foundation grant 75074 GA AGR 7621, a PHS grant AI-14509, and a Charles and Johanna Busch award. We thank Mrs. R. Shamy for preparation of the electron microscopy plates.

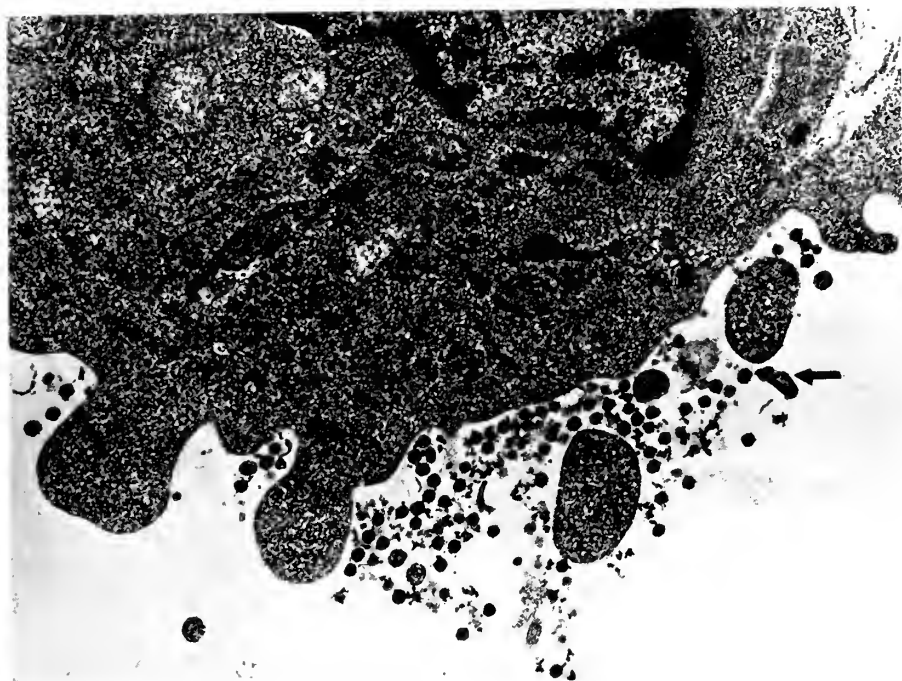


Fig. 2. Extracellular abundance of C-type particles following inoculation of VSW with *A. californica* NPV. A virus particle (arrow) can be seen with partially removed envelope. $\times 45,000$.

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TWO NEW SPECIES OF *LACCOBIUS* FROM
EASTERN NORTH AMERICA (COLEOPTERA: HYDROPHILIDAE)

Stanley E. Malcolm

Abstract.—*Laccobius reflexipenis* and *L. spangleri* are described from eastern North America. Holotypes and paratypes are designated. Male genitalia and pronotal maculation are figured. Distribution maps are included.

In "The Water Beetles of Maine" (Malcolm, 1971) I mentioned two species of *Laccobius* to be described by two other taxonomists, Brian S. Cheary and Ronald B. Willson. Because my paper included significant characters and appeared while those of Cheary and Willson were in press, I inadvertently became descriptor of the two species. In order to clarify this unfortunate situation, I include full descriptions of the two species and designate types. The publications of Cheary and Willson have not yet appeared.

The following standard abbreviations for collections are used: BMNH—British Museum (Natural History); CAS—California Academy of Sciences; CNC—Canadian National Collection; DCM—David C. Miller; FMNH—Field Museum of Natural History; SEM—Stanley E. Malcolm; UCR—University of California at Riverside; UM—University of Maine; USNM—U.S. National Museum of Natural History.

Laccobius reflexipenis n. sp., Malcolm

Laccobius reflexipenis "Cheary." Malcolm 1971. Univ. Maine Agri. Exp. Sta. Tech. Bull. 48:40-42.

Holotype. Male; Maine, E. Corinth, Penobscot Co. July 17, 1969, Stan Malcolm; USNM type number 71356.

Form oval; length 2.8 mm; width 1.7 mm; head with frequent medium sized punctures overlying a strongly microreticulate surface, color metallic bronze-green except a triangular pale area anterior to the eye; pronotum punctured and reticulate as head, disc metallic bronze-green, margins pale, (for pronotal spot pattern see Fig. 1a); scutellum metallic bronze-green; elytra pale, medium sized dark brown punctures arranged in imperfect series overlying moderately microreticulate surface, some puncture marks coalesced along suture at midpoint to form a dark spot, punctures at apices and margins only slightly darkened; ventral surface dark brown, covered with dense hydrofuge pubescence; coxae dark brown, trochanters and fem-

A →



B →

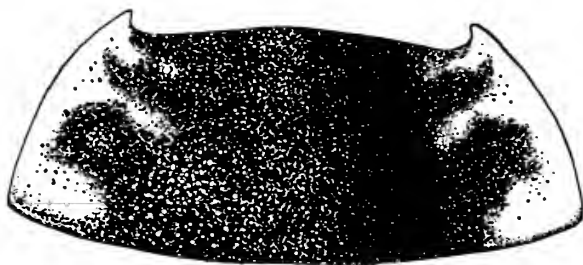


Fig. 1. Pronotal spot patterns: a. *Laccobius reflexipennis* Malcolm, b. *Laccobius spangleri* Malcolm.

ora brown except lighter at distal ends, tibiae and tarsi pale, forefemora with dense hydrofuge pubescence on proximal third; palpi and antennae pale except antennal club brown; aedeagus with median lobe filiform, bowed in lateral view; parameres with recurved extensions in ventral view, tips of parameres downcurved, rounded (Fig. 2a).

Variation. Length 2.4 to 3.4 mm, males average 2.6 mm, females 3.0 mm; metallic colored areas often bronze-red, sometimes brown; pale background coloration often darker, obscuring pronotal spot pattern and changing (often enhancing) elytral maculation. The great variation between individuals in coloration and size necessitates the use of male genitalia to distinguish *L. reflexipennis* from sympatric species.

Specimens examined. 323; Distribution is plotted on map 1. Paratypes bearing the cited locality data have been deposited in the following collections: 1 ♂, 1 ♀, Indiana, U.S.A., Starke Co., W. S. Blatchley Coll. (BMNH); 2 ♂, Mo. Ripley Co., Buffalo Creek at Route C, 5.5 mi N. of Briar, 5-VIII-1967, collector H. B. Leech (CAS); 1 ♂, Boiestown, N. B.,

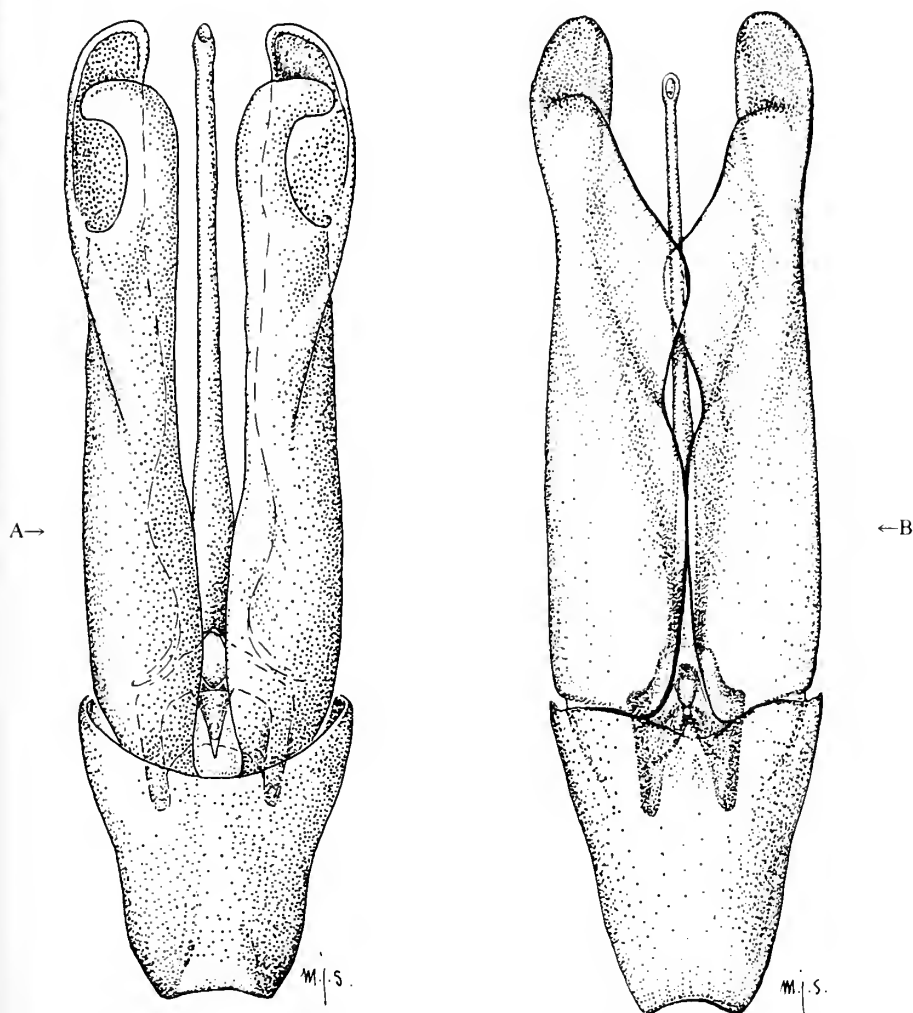


Fig. 2. Male genitalia, ventral view: a. *Laccobius reflexipenis* Malcolm, b. *Laccobius spangleri* Malcolm.

VII-11-1928, W. J. Brown, 1 ♂, Knowlton, Que., VI-26-1928, G. H. Fisk (CNC); 1 ♂, MAINE, Corinth, Penobscot Co., 8-13-1969, Stan Malcolm (DCM); 1 ♂, IOWA, Scott Co., Davenport, V-10-1964, leg. S. B. Peck (FMNH); 1 ♂, 1 ♀, E. of Beddington, ME, VIII-1-1970, Rt. 9, Stan Malcolm (SEM); 1 ♂, Indiana, U.S.A., Starke Co., W. S. Blatchley Coll. (UCR); 2 ♂, MO., 7 mi W. of Weldon Spgs., VI-25-1954, Paul Spangler, 1 ♂, 8 mi W. Steelville, MO. Meramec River, X-10-1953, M. C. Grabau (USNM).



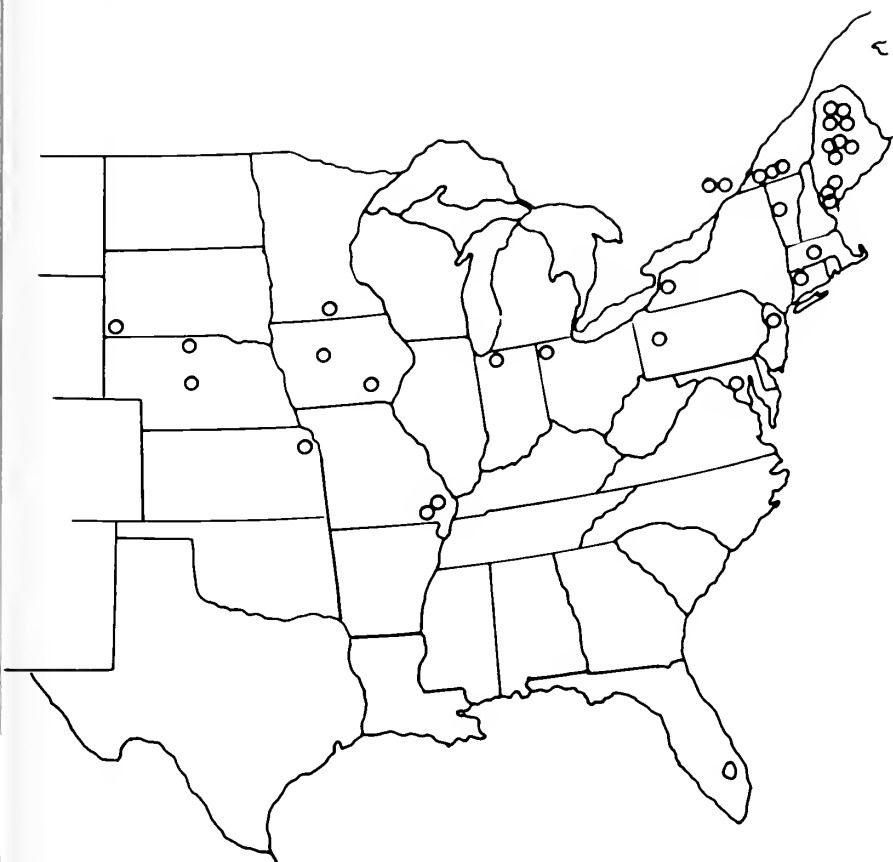
Map 1. Distribution of *Laccobius reflexipennis* Malcolm.

Laccobius spangleri n. sp., Malcolm

Laccobius spangleri "Willson." Malcolm 1971. Univ. Maine Agri. Exp. Sta. Tech. Bull. 48:40-42.

Holotype. Male; Dixmont Ctr., Maine VII-20-1970, S. Malcolm; USNM type number 73365.

Form oval; length 2.5 mm; width 1.6 mm; head with frequent medium sized punctures overlying a strongly microreticulate surface, color metallic bronze-green except a triangular pale area anterior to the eyes; pronotum punctured and reticulate as head, disc metallic bronze-green, margins pale, (for pronotal spot pattern see Fig. 1b); scutellum metallic bronze-green; elytra pale, medium sized metallic bronze-green punctures arranged in im-



Map 2. Distribution of *Laccobius spangleri* Malcolm.

perfect series alternating with less regular rows of punctures overlying lightly microreticulate surface, some puncture marks coalesced along suture at midpoint to form a dark spot, other vague dark spots similarly formed distributed in a pattern typical of many *Laccobius* species, punctures at apices and margins with little darker marking; ventral surface and coxae dark brown, covered with dense hydrofuge pubescence; legs brown proximally, gradually lighter from mid-femora distally, forefemora with dense hydrofuge pubescence in basal third; palpi and antennae pale except antennal club brown; aedeagus with median lobe filiform, bowed in lateral view; parameres with overlapping semi-membranous extensions in ventral view, tips of parameres downcurved, rounded, concave below (Fig. 2b).

Variation. Length 2.3 to 3.2 mm, males average 2.6 mm, females 2.9 mm; metallic colored areas often bronze-red, sometimes brown; background coloration may be lighter or considerably darker than holotype, obscuring pronotal spot pattern and changing elytral maculation. As with the preceding species, the great variation between individuals in coloration and size necessitates the use of male genitalia to distinguish *L. spangleri* from sympatric species.

Specimens examined. 454; Distribution is plotted on map 2. Paratypes bearing the cited locality data have been deposited in the following collections: 1 ♂, 1 ♀, Indiana, U.S.A., Starke Co., W. S. Blatchley Coll. (BMNH); 1 ♂, 1 ♀, 7-VII-1946, Cornwall, CONN., Spring Brook, Chamberlain Collector (CAS); 1 ♂, 1 ♀, Ottawa, Ont., 15-V-1930, W. J. Brown (CNC); 1 ♂, 1 ♀, Dixmont Ctr., ME., VII-20-1970, S. Malcolm (DCM); 1 ♂, 1 ♀, MAINE, Oxbow, Aroostook Co., July 7, '69, Stan Malcolm (SEM); 1 ♂, Mohawk, MICH., Gratiot River, Keweenaw C., 7 July 1964, R. B. Willson. 1 ♂, Allendale, MICH., Ottawa Co., 17 July 1963, R. B. Willson (UCR); 2 ♂, MAINE, Harmony, Somerset Co., Aug. 3, 1969, Stan Malcolm (UM); 1 ♂, 1 ♀, 4 mi E. Levering, Emmet Co., Mich. 43b, VIII-5-1952, Paul J. Spangler (USNM).

For both species the male genitalia are diagnostic. Males can be recognized by their generally smaller size and dilated second foretarsal segment. As with many species of *Laccobius*, females can only certainly be determined by association with males. The pronotal spot pattern is variable, but may be of use in separating these species from other *Laccobius*. In Maine I have collected these species together and with *L. minutoides*. D'Orchymont (1942) included a figure of the male genitalia in his description of *L. minutoides*.

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THE EVOLUTION OF EYESPOTS IN TROPICAL
BUTTERFLIES IN RESPONSE TO FEEDING ON
ROTTING FRUIT: AN HYPOTHESIS

Allen M. Young

Abstract.—A substantial portion of the butterfly species in tropical forests of Central and South America feed primarily as adults, on rotting fruits and to a lesser degree, on moldy (fermenting) sap issuing from wounds in trees. In general, exploitation of fruit frequently occurs on the ground, where volatile odoriferous substances, released in decay, attract butterflies in the three nymphalid subfamilies Satyrinae, Brassolinae, and Morphinae; similarly, sap and hanging injured or rotting fruit are exploited arboreally by several genera of the Nymphalinae. However, a few nymphalines also feed on fallen fruit and experimentally placed fruit baits on the ground. This paper explores in a preliminary way the possible adaptive relations between (1) feeding on the ground versus feeding arboreally, (2) dispersal agents (vertebrates) as opportunistic predators of feeding butterflies, (3) functional role of eyespot markings (eyespot) on the undersides of wings, and (4) impairment of escape behavior of butterflies from intoxication acquired by feeding on rotting fruits. The general thesis is advanced that butterflies become intoxicated in nature from feeding on rotting fruits, and that eyespots increase the margin for successful escape when normal behavior has been impaired. Since fallen fruits ferment quickly, the intoxication of butterflies is greatest on the forest floor and eyespots are most prevalent in the brassolines, satyrines, and morphos, the three groups that thrive here. Very often, feeding takes place in patches of forest floor directly exposed to sunlight, and at times of the day when such exposure is maximized. Under conditions of direct sunlight, eyespot markings are very noticeable. A high selective value is placed on eyespots as an additional line of evasive escape behavior since animals attracted to fallen fruit (for dispersal purposes and feeding on insects) can be predators on butterflies. Eyespots are known to lure pecking and biting away from the body of a butterfly or moth. Alternatively, it is also known that eyespots frighten away animals. Either way, they function to reduce the likelihood of attack on an insect by a vertebrate predator. It is easy to conceptualize how the three groups of butterflies developed similar eyespots as they are closely linked phylogenetically. For the arboreal-feeding nymphalines, eyespots are expected to be less functional as indicated by their conspicuous absence in most species. Such markings are also generally absent from most flower-visiting butterflies. The decomposition of fallen fruits and the yeasting of sap flows are processes that play a major role in maintaining the butterfly community of tropical forests.

As microbes render fruit less savory for vertebrates that act as dispersal agents, they open a feeding niche for butterflies.

Introduction

Each year, the lowland tropical rain forests of Central and South America contain collections of fallen fruits from various tree species. Most of these, such as *Coumarouna oleifera* (Leguminosae) are sweet-smelling rotting, fleshy fruits which attract a variety of butterflies, predominately in the nymphalid subfamilies Satyrinae, Brassolinae, and Morphinae (e.g., Young 1972a). Two major features of these interactions between fruits and butterflies are: (a) although the fallen fruit collection can be large under a parent tree, only certain fruits are returned to repeatedly by butterflies, and (b) an individual of a butterfly species participating in the interaction often returns to the site many times over several days or weeks. The observed extension of the proboscis on, or into, the fruit indicates that the butterfly is ingesting fluids seeping from the fruit.

After a fruit matures, it generally falls to the ground where it sits for some period that may be terminated by dispersal away from the area by a vertebrate (Smythe 1970); if such dispersal does not occur, the ripe fruit spoils and begins to rot as a result of microbial action on the fruit wall. Spoilage is usually accompanied by the emission of a sweet or tangy odor from the fruit. At this stage, the fruit becomes a feeding patch for many insects, including butterflies.

The selective advantages for microbe species to attack fallen fruits prior to the onset of dispersal by vertebrates have been discussed (Janzen 1977). Along with the microbes causing the decay, the insects associated with these fruits, including Lepidoptera, are also conceptualized as being in competition with vertebrates (fruit and seed dispersal agents) for the fruit as a food resource (Janzen 1977). Although the feeding on rotting fruits and fermented fruit products by Lepidoptera and other insects has been documented extensively (e.g., Dethier 1947; Frost 1928; Norris 1936; Barcant 1970; Gilbert 1972; Muyschondt 1973a, b; Young 1972a; Gomez 1977 and many others), little attention has been given to the likely ecological consequences of such feeding behavior. The purpose of this note is to call attention to some possible features of these interactions that relate to a predicted loss in fitness resulting from such feeding, and the role of cryptic coloration and behavior of day-flying Rhopalocera in offsetting these effects. These comments are made as an argument for further documentation of these interactions, especially in the tropics.

Unusual Butterfly Foods

Adults of many temperate and tropical butterflies imbibe juices from ripe fleshy fruit, and rotting fleshy fruits (e.g., Comstock 1895; Young 1972a). In the American tropics, many forest-dwelling satyrines, brassolines, and morphos, exhibit this behavior (Brown 1972). In addition, many nymphalines visit fresh arboreal sap flows (e.g., Muysshondt 1973a, b). In general, Nymphalinae such as *Anaea*, *Prepona*, *Adelpha*, *Historis*, and *Marpesia* exhibit this behavior. Among the brassolines, genera such as *Caligo*, *Brassolis*, and *Opsiphanes* have been observed to visit rotting fallen fleshy fruits (e.g., Harrison 1963; Young 1972a; Young and Muysshondt 1975). In addition to feeding on rotting fleshy fruits, both under natural conditions and when baited (Young 1972a; Young and Muysshondt 1973; Young 1973; Young and Thomason 1974; Young 1975), *Morpho* has also been seen imbibing fluids from moldy growths on sap flows of fallen trees (Young and Muysshondt 1973 and Fig. 1). Furthermore, *Morpho* feeds on yeasts associated with disposed dairy products in garbage heaps at the edge of forest at the Monteverde farms in Costa Rica (anonymous).

An outstanding morphological feature of the Satyrinae, Brassolinae, and Morphinae, generally absent in the Nymphalinae and of significance in feeding behavior, is the presence of distinctive eyespots on the undersides of the wings (Fig. 1). In addition to being generally absent from the Nymphalinae, including genera that feed arboreally on sap flows, these markings are absent from most flower-visiting butterflies. Owing to the positioning of the wings in a vertical closed position while feeding (Fig. 1), the eyespot markings (eyespot) are exposed maximally to the visual field of an approaching vertebrate. All four subfamilies of fruit-and-sap-feeding butterflies are cryptically colored in terms of the background coloration of the undersides of the wings.

Spatial Temporal Variation of the Butterfly Community

Owing to the very great diversity and local species abundance of nymphalines, brassolines, and morphos in the wet forests of tropical America, it seems that the exploitation of ripe or rotting fleshy fruits and fermenting sap flows is a significant factor in determining and maintaining this subset of the butterfly community in a forest habitat. The Morphinae and Brassolinae are strictly tropical groups, while most Satyrinae are also strictly tropical (Ehrlich and Raven 1965). Furthermore, the Nymphalinae are relatively far more abundant in the tropics. In southern Brazil, nymphalines, morphos, satyrines, and brassolines reach very high levels of diversity and many members of these groups exhibit little or no seasonal variation in abundance at a locality throughout the year (Brown 1972). Thus the subset of the adult



Fig. 1. Above: live individual of *Morpho peleides*, wild-caught in northeastern Costa Rica. Note vertebrate-type eyespots on the undersides of both sets of wings. Below: *Morpho peleides* feeding on soupy fungal growth on sap issuing from a fallen tree in northeastern Costa Rica. Time of day is late afternoon; eyespots fully exposed while feeding.

butterfly community associated with ripe and rotting fleshy fruits and moldy sap flows is generally active throughout much of the year, and this is also the case for the northeastern tropical wet lowland forest region of Costa Rica (pers. obs.), and presumably along much of the Atlantic watershed region of southern Central America.

Owing to the generally high spatial patchiness of parent individuals of many tree species in tropical forests (e.g., Black et al. 1950), and the seasonality of fruit production in many of these species (Frankie et al. 1974), rotting fallen fruits for butterflies are expected to be a variable resource from place to place, and from time to time at a given place. Thus the butterflies are expected to exploit a succession of fruit species in space and time as availability of each fruit species changes; during periods of peak fruit production of a preferred species, and at places where the fruit is abundant, it is predicted that populations of butterfly species exploiting this food supply will be residential.

Young (1972a) found that individuals of a given species of satyrine, brasoline, or morpho tend to return to the same fruit baits over several days. Observations such as these and others for *Morpho* (e.g., Young 1973; Young and Thomason 1974) suggest indirectly that the food niche of these butterflies is probably narrow at a given time of the year. The observed tendency for individuals to return repeatedly to the same area of fallen fruit or bait each day (e.g., Young 1972a; Young and Thomason 1974) suggests that these butterflies become familiar with certain portions of the habitat where food resources are found; there is less of a tendency to wander through large areas and rather more of a tendency to become localized near food supplies. What the relationships, if any, of such distributional patterns have to locations of larval food plants has not been determined. In general, though, these observations and those of the preceding paragraph suggest that the subset of the tropical forest butterfly community using rotting fruits and moldy sap flows is a fairly predictable collection of species in space and time. Such conditions may increase predation by home-ranging small vertebrates on adults.

Cryptic Properties of Adult Tropical Butterflies

Cryptic wing coloration in the Lepidoptera evolved as a means of allowing adults to match the surrounding environment (e.g., Wickler 1968). Most of the Neotropical fruit-eating groups such as the morphos, brassolines, and satyrines possess distinct eyespots on the undersides of the wings. These eyespots closely resemble vertebrate eyes, and several of them often occur on the wings (Fig. 1). In direct light, the eyespots are very noticeable to the human observer, while in shade they tend to blend in with the cryptic background hues of the wings, and of the forest floor. It is believed that such markings stimulate pecking by birds away from the body (Blest 1957; Wick-

ler 1968). Such markings presumably lower the risk of an individual butterfly being eaten while resting or feeding with the eyespots exposed to the visual field of predators. These markings, in combination with generally subdued colors and generally motionless posture while feeding or resting, are effective deterrants for vertebrate predators. It is also known that eyespots frighten away some animals, rather than inviting attack (e.g., Hailman 1977). It is not known which of these types of interactions occur in tropical butterflies feeding on the forest floor, but the frequent occurrence of individuals with uncanny symmetrical sections missing from the hindwings in *Morpho* and *Caligo* suggests that these insects are attacked by small vertebrates (reptiles) while feeding or resting.

With a few exceptions, such as *Prepona*, most Neotropical nymphalines lack eyespots. Yet the general coloration of the undersides of the wings is subdued and cryptic; feeding proceeds generally arboreally from moldy sap flows (e.g., Muyshondt 1973a, b). It appears, therefore, that the occurrence of small eyespots is most frequent among Neotropical butterfly groups that feed on or near the ground in forest habitats, these being the Morphinae, Brassolinae, and Satyrinae.

In general, there is a burst of butterfly feeding activity just before sunset on clear, sunny days in Costa Rican lowland tropical rain forests (pers. obs.). While sections of the forest floor receive varying amounts of direct sunlight during the day and butterflies feeding on rotting fruit sometimes sit in patches of sunlight, Hailman (1977) mentions that Daniel Janzen has noted that direct sunlight is almost horizontal near sunset in tropical forests. Thus near-sunset feeding in butterflies may also occur in patches of direct sunlight. These conditions enhance the visual perception of eyespots by vertebrate predators while the butterflies are feeding.

Some recent data from temperate zone forests indicate that vertebrates that disperse the fallen fruits of some tree species are most active in areas where direct sunlight is more abundant (Thompson and Willson 1978). Damage of fallen fruit by various invertebrates was cited as the major selection pressure favoring rapid dispersal of fruit in that study. Thus, a similar pattern may exist in tropical forests, where light gaps and other types of exposed areas are common. This means that small vertebrates which disperse fruit and are opportunistic predators of butterflies, could be active in sunny places where feeding butterflies maximize exposure of eyespots while feeding.

Intoxication and Modification of Behavior

Fallen ripe fruits are attacked by a wide variety of microbes, these organisms producing toxins, antibiotics and other mechanisms of substrate degradation that result in fruit spoilage or rotting (many references in Janzen 1977). This rotting or fermentation releases volatile substances that attract

insects, including many Lepidoptera; fermenting fruit juices become available as food for butterflies as the result of seeping through breaks in the fruit wall, or from general seepage through a decaying fruit wall. Rotting fruits and moldy (yeasty) sap flows are common sources for the isolation of yeasts, which are specialists on eating ripe fruit (Janzen 1977), this interaction forming the basis for feeding by butterflies. While the spoilage of the fruit makes it less available to vertebrates, it becomes a major resource for butterflies.

It is not known exactly what kinds of nutrients butterflies obtain from rotting fruits or moldy sap flows, but alcohol is imbibed since some species exhibit intoxicated behavior after feeding (e.g., Gomez 1977). There are far more observations of occasional intoxication of birds and mammals from feeding on rotting fallen fruits, rendering them easier to capture (Janzen 1977). Owing to the high humidity of the lowland tropical rain forest and the relatively small body size (and nervous system) of insects, it is likely that intoxication in butterflies is more widespread than for larger animals exploiting these food sources. Adults of *Morpho peleides* with abdomens prodigiously distended and swollen, as the result of extended periods of feeding at baits of rotting bananas, are unable to fly away when disturbed (pers. obs.). In some instances where feeding is less intense at baits, adults fly away but with great difficulty, making them very easy to capture with a net (pers. obs.). My experience with bait studies of *Morpho* and *Caligo* in Costa Rica from 1968 through 1976 is that the longer adults are left undisturbed feeding at these fruits (usually bananas) the greater the level of apparent intoxication as reflected in the impairment of typical escape behavior. Butterflies, when recently arrived at a bait and disturbed, do not exhibit such modified behavior, presumably because there has been insufficient feeding for intoxication to occur. When intoxicated butterflies such as *Morpho* and *Caligo* are picked up, they excrete large quantities of fluid; when left undisturbed for a period, most fluids are excreted and eventually these individuals "sober up" and fly away.

For morphos and brassolines the sequence of events in typical escape behavior elicited when they are deliberately disturbed, shortly after arriving at a bait, is a brief period of rapid, jerky wing movements followed by walking and flight. When disturbed following considerable feeding, the behavioral sequence is to remain motionless and then an attempt to fly away. In some instances, a heavily intoxicated *Morpho peleides* remains motionless even after an aerial net is placed over it. As with other animals, symptoms of intoxication in butterflies include the tendency to sit quietly, apparently the result of depression of the nervous system. A consequence is that recovery time is extended and it is this interruption of the typical escape behavior that renders intoxicated butterflies easy prey for vertebrates.

Intoxicated butterflies are frequently discovered at fruit baits deliberately

placed in small piles on the forest floor (e.g., Young 1972a; 1973; Young and Thomason 1974) whereas butterflies observed at natural food supplies are seldom intoxicated (e.g., Young 1975). Therefore, the frequency of severe intoxication under natural conditions is questionable. Introduced baits, several centimeters across and placed close-by in an area represents a highly available food supply as most natural supplies come in smaller patches and the patches are very dispersed. Thus although the fallen fruits of *Coumarouna* trees are abundant seasonally and attract *Morpho amathonte*, *Morpho peleides*, and many satyrines, the sweet-smelling pulpy cover on each fruit occurs as a thin coat and this coat generally dries up in a few days. Other natural food supplies include small, yeasty fresh sap flows at the base of large forest trees (Young 1975) attracting *Morpho* and several Satyrinae.

The single exception to these observations would be the availability of large quantities of rotting banana (*Musa* (Musaceae)) in plantations, and areas where there are extensive plantings of other fruit trees such as mango (*Mangifera* (Anacardiaceae)) and guava (*Psidium* (Myrtaceae)). In these habitats, large quantities of rotting fruit are available to butterflies for several months each year, and intoxicated individuals of *Morpho* and *Caligo* have been seen (pers. obs.).

Patterns of Butterflies at Fruits

As the result of capture-mark-resight field studies, it has been found that by far the majority of individuals appearing at both experimental and natural rotting fruits and moldy sap flows for *Morpho*, *Caligo* and several satyrines (e.g., *Antirhea*, *Piriella*, *Caerois*, *Taygetis*) are males (Young 1972a; Young 1973; 1975; Young and Muyschondt 1973; Young and Thomason 1974; pers. obs.). Females tend to show up more irregularly than males (Young 1972a). The scarcity of females at natural food supplies in forest habitats is less understood. But Young and Thomason (1974) found that females of *Morpho peleides* were far less abundant than males at fallen fruits of *Guazuma ulmifolia* Lam. (Sterculiaceae). A similar pattern of abundance between the sexes was seen on the sap flows of *Samanea saman* Merrill (Leguminosae) for the same population at a different time (Young 1975). The sex ratio of laboratory-reared *Morpho peleides* is unity (Young and Muyschondt 1973). It seems, therefore, that for at least *Morpho peleides*, there is a definite behavioral difference in feeding activities between males and females. The observed general tendency for males to predominate at bait for several species of satyrines and brassolines in addition to morphos, suggests that such a behavioral difference is widespread among these butterflies, although more data are needed to confirm this prediction.

In addition to the above considerations in relation to feeding, eyespots undoubtedly function to enhance survival from predators while butterflies

are resting. As with feeding on the ground, morphos, satyrines, and brassolines generally spend the night hanging from leaves near the ground (pers. obs.). During these periods the butterflies are exposed to nocturnal vertebrate predators such as lizards and small mammals.

Discussion

Although many insects including some nymphalines of temperate zones exploit rotting fruits and moldy sap flows (e.g., Simon and Enders 1978), such feeding behavior is more prevalent in the American tropics, where members of four major subfamilies of nymphalids, the Nymphalinae, Morphinae, Brassolinae, and Satyrinae (following Ehrlich 1958), contain genera and species whose adults feed almost exclusively upon these food sources. While it is known that some temperate-zone families of Lepidoptera are attracted to volatile fermentation products (e.g., Utrio and Eriksson 1977), less is known about the attraction of tropical butterflies to rotting fruits and moldy sap flows. Bait studies indicate that butterflies become intoxicated from extended periods of feeding on an abundant fruit supply and fruit products (i.e., large resource patch). Although intoxication is less likely for butterflies exploiting natural food sources which tend to be smaller and dispensed in space and time, it is expected that some individuals of a species would experience intoxication, thus increasing the likelihood of being detected by predators. In addition to insects being attracted to these food sources, vertebrate predators may also be attracted to rotting fruit and moldy sap flows. Such conditions favor the evolution of morphological crypsis and associated behavior patterns that provide effective passive protection of intoxicated individuals.

Although the functional role of eyespots on the undersides of lepidopteran wings has been examined (e.g., Stradling 1976), I wish to advance a new hypothesis to account for the adaptive role of these markings. The small eyespots so familiar on many different species of satyrines, brassolines, and morphines, and the noticeable lack thereof in most nymphalines (including fruit and sap-feeding forms) suggests that they function to provide additional protection for butterflies feeding from the forest floor; butterflies generally feeding arboreally, including most nymphalines that feed on moldy sap flows, lack eyespots, suggesting that such markings are less adaptive to butterflies in these feeding niches. Owing to the increased likelihood that rotting fruits have already fallen from the parent tree by the time they are degraded to suitable food for butterflies, most incidents of intoxication probably occur on the forest floor. Here, the eyespots (Fig. 1) provide additional protection to an individual butterfly that perhaps is partially intoxicated to a point of impairment of escape behavior. If such markings act as effective decoys for pecking by birds and flash attacks by other vertebrate predators, they provide additional time for an escape.

Owing to the close evolutionary history of the Satyrinae, Brassolinae, and Morphinae (Miller 1968), eyespots probably evolved in one of these groups and were then carried over to the others as they evolved. It is less clear as to how these markings, so strikingly similar among most members of these three groups, could have also evolved in the Nymphalinae, a very large group exhibiting manifold patterns of resource exploitation, both as larvae and adults. Most members of the Morphinae as well as all members of the Satyrinae and Brassolinae are monocot-feeders as larvae (Ehrlich and Raven 1965; Miller 1968). Virtually all Nymphalinae are dicot-feeders (Ehrlich and Raven 1965). Although it is difficult to determine whether or not the Brassolinae and Satyrinae were derived phylogenetically from the Morphinae, or the reverse (e.g., Young 1972b; Ehrlich and Raven 1965; Durden and Rose 1978), the three groups are closely linked in evolutionary history.

The collections of fallen, rotting fruits available each year in the tropical wet forests are a major food resource for many butterflies, and the abundance and local diversity of these insects may be determined in part by these resources. The various sweet-smelling to fermenting odors given off by these fruits attract butterflies and other insects, and the activities of these animals in turn hasten the decay processes, making the fruit less attractive to larger animals (Janzen 1977). In terms of the insects, the fruits are a predictable resource in time and space and such predictability may be a major selective factor in the establishing of breeding populations of individual species in a region of tropical forest. The repeated exploitation of a fruit crop in an area by the subset of the butterfly community that feeds on fruits reduces the likelihood that these fruits will be carried away from the area by larger animals acting as dispersal agents. As discussed primarily for microbes associated with rotting fruit (Janzen 1977), the butterflies and other insects are entering a competitive interaction with larger animals for this food supply. Such interactions are less likely at arboreal sap flows, although both resources are probably limiting factors for butterflies. Thus the likelihood that opportunistic predators on large insects (reptiles, birds, and small mammals), will be active near or at fruits on the forest floor is greater than for arboreal sap flows; such conditions select for behavior and morphological adaptations that increase the survival of the butterflies feeding on the fruits.

Eyespot markings have high adaptive value under these conditions, and females are less abundant in such places since males are the more expendable. If mortality of feeding butterflies is high, selection favors more cryptic behavior in females. Although the high levels of intoxication of butterflies at fruit baits and fruit products (e.g., Gomez 1977) are probably not frequently attained in nature, save for the exploitation of fallen fruit in banana plantations, there exists a spectrum of intoxication levels affecting escape behavior. Breakage of the wall of a fruit by rotting, falling, or handling by

animals allows fruit-foraging butterflies to use the fruit as a food source, but at the same time it exposes a portion of the population to intoxication which in turn lowers fitness. This interaction is mediated by the microbe community associated with the fruit. As discussed primarily for the microbes (Janzen 1977), the joint activities of dispersal agents (vertebrates) affects fitness in the populations of the plant (tree) species involved.

The ideas developed in this paper on the adaptive significance of butterflies feeding on rotting fruits and fermenting sap flows in the tropics may also be applicable to the temperate zone fauna. For nymphalids of the temperate zone that feed on sap flows and only occasionally on rotting fruit, there is a lack of eyespot markings. Most of these feed arboreally and the density of vertebrate predators is very likely lower than in comparable tropical habitats. Selection pressures favoring eyespots are expected to be most intense in the tropics, and to be most prevalent among butterflies that feed on rotting fruits on the forest floor. Given the great diversity of butterflies in the tropics, the occurrence of eyespots in three large groups, such adaptations may have high selective value hitherto underemphasized.

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NEST OF THE WASP *CLYPEARIA WEYRAUCHI*
(HYMENOPTERA, VESPIDAE)

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Abstract.—The nest of the Neotropical social wasp *Clypearia weyrauchi* Richards is described for the first time. It consists of a single comb of sessile cells built directly on a tree trunk and covered by a domed envelope with an entrance below the center. The envelope does not contact the comb and is not thickened. It is unusual in having its outer surface coated with a layer of transparent film, probably a glandular secretion. This film serves to strengthen the crumbly, granular carton, which consists primarily of stone cells. The same film coats and strengthens the cell walls. Despite the fact that one of the two colonies examined appeared to be completing its cycle, its nest had not been enlarged beyond its initial size, a rare phenomenon among social wasps.

There are two reasons why the study of social wasps' nests is important. First, since the nest serves as a boundary between the external and internal environments of the colony, it must be considered in any study of the behavioral ecology of a species. Second, since nest construction behavior evolves, and since many of the details of nest architecture are species specific, nests provide valuable behavioral input into phylogenetic studies of the social Vespidae. Though the range of diversity of major architectural types is known (Jeanne, 1975), for studies of the behavioral ecology and phylogeny of the wasps we need to know such details as the type of cell construction, manner of thickening the envelope, material used, texture and strength of the carton, and the extent of the use of oral secretion in the nest. This kind of knowledge exists for the nests of only a small fraction of the approximately 700 species of social wasps. The Neotropical social wasp genus *Clypearia* comprises seven species (Richards, 1978); the nests of two, *C. apicipennis* and *C. angustior*, are known (Ducke, 1910; Araujo, 1951), though Ducke's description of the nest of *C. apicipennis* was limited to one sentence. The purpose of the present paper is to describe the nest of a third species, *C. weyrauchi* Richards. All three species construct a single comb of cells directly on the surface of a tree trunk or limb, and cover it with a single-layered envelope, but the nest of *C. weyrauchi* differs in several interesting details from those of its congeners.

The following description is based on two nests collected near Santarém, Pará, Brazil (2°32'S, 54°20'W). Both were located in the same grove of trees

standing in a brushy pasture at the edge of the *varzea* (annually inundated floodplain of the Amazon River).

The larger of the two nests (no. 1112) was collected at night on July 26, 1975. It was situated at a height of about 7 m on the underside of a large horizontal branch. Though well sheltered from rain, the nest was not obscured by foliage. The nest was 45 cm long by 18 cm wide and contained approximately 1000 cells. This colony was evidently in the last stages of decline, for the nest contained only 12 adults and the brood cells were empty except for a few scattered pupae. The second nest, illustrated in Fig. 1, was collected from a nearby tree of the same species before dawn on August 14, 1977. It was also approximately 7 m high and very exposed, but the colony had chosen a nearly vertical section of tree trunk. The nest was 25.5 cm long by 9 cm wide and contained 287 cells. The adult population comprised 74 females, and the cells contained brood in all stages of development.

Envelope

The envelopes were constructed entirely by the edge construction technique, the primary form of construction of all vespid nests so far described (Jeanne, 1973). At no point were the envelopes thickened by the addition of pulp to their surfaces. The thickness of the carton varied between 0.75 and 0.85 mm.

The absence of surface thickening means that the pattern of construction of the envelope remains unobscured. This pattern is due to the lines of growth representing individual loads of carton pulp added by the wasps, and is visible in Fig. 1. The pattern for each nest indicates that the envelope was built at the outset to its final size, and was not enlarged from a smaller original envelope. In the smaller nest (Fig. 1) the lines of growth indicate that the envelope was raised uniformly around the entire comb to a height of 1.0–1.5 cm, but that then carton was added to the two ends, and especially the upper end, faster than at the sides. The entrance, which results from the incomplete closure of the envelope, is consequently positioned below the middle of the nest. In the smaller nest the entrance was 1 cm in diameter. There was no thickening of the carton around the rim of the entrance, nor was there any flaring outward of the rim to form a tube or spout.

The larger nest had two entrances. The pattern of growth lines around one of these was very irregular, suggesting that this part of the envelope had been damaged and repaired, leaving the second entrance.

The envelope was constructed of a non-fibrous, finely granular material. Under the dissection microscope the individual particles could readily be broken up into finer granules 0.01–0.02 mm in diameter. These appear to be stone cells, most commonly found in the cortex of young stems, bark, and in fruit and seed coats (R. C. Koeppen, personal communication). Micro-

scopic examination also revealed minute amounts of an almost clear, plastic-like film intermingled with the particles and serving to bind them loosely together. This substance is probably a salivary secretion that is mixed with the particles as they are masticated before being applied to the nest. This matrix is very weak and the resulting carton very crumbly.

The envelope is given added integrity by a thin surface coating of what is presumably more of the same salivary secretion. This material is evidently added after the envelope is completed, for it forms a discrete film on the outer surface of the carton, even extending for several mm onto the adjacent substrate.

It is this thin pliable film that gives the envelope what little strength it has. Flexing the envelope readily cracked the carton, and with a minimum of abrasion of the uncoated inner surface the carton crumbled away, leaving only the outer film and a few scattered particles of carton adhering directly to it. At the time of collection of each nest there were several such "windows," some several cm across, that appeared to have originated by such loss of the underlying carton (Fig. 1). It is not known whether these windows were intentionally produced, or whether they simply resulted from wear and tear.

The intact nests *in situ* were rather inconspicuous. This was partly because the sloping sides of the envelope helped eliminate shadows, and partly because the nest closely matched its substrate in color. The close color resemblance of carton and bark, and the fact that the carton is composed largely of stone cells, suggest that the source of carton material might have been the bark of the tree on which each colony nested. The translucent coating of secretion over the envelope further subdued any contrast between the nest and the tree trunk.

Comb and Brood

The comb of each nest was centered within the space enclosed by the envelope. A space of 1.3–4.5 cm separated the edge of the comb from the line of attachment of the envelope to the substrate. Thus the envelope is not initiated by the elongation of the walls of peripheral cells, but is built up from the substrate completely independently of the comb (Fig. 2).

The combs of both nests appeared to have been built in a single effort; there were no irregularities in outline, hexagonal pattern, cell height, or brood distribution to indicate that a smaller original comb had been enlarged.

All cells in both nests were sessile; that is, they were built directly on the surface of the tree trunk, which formed the bottoms of the cells (Jeanne, 1973). Cells were 5.2–5.4 mm in diameter and reached a depth of 20 mm. Those of the nest on the vertical trunk were angled downward 15° with respect to the trunk surface (Fig. 2).



Fig. 1. Intact nest of *Clypearia weyrauchi* (no. 2035). The nest is 25.5 cm long. The striations indicate the pattern of construction of the envelope, and converge on the entrance. The dark blotches above the envelope are 'windows' formed by the removal of carton, leaving only the translucent film coating the outer surface of the envelope.



Fig. 2. The nest shown in Fig. 1 with its envelope removed. The line of attachment of the envelope is visible on the bark surface. The comb is centered within the surface enclosed by the envelope, and does not contact the envelope.

The cells were constructed of the same crumbly carton as the envelope, and were similarly coated with a film of secretion. Thus the walls of the cells were layers of carton sandwiched between two layers of secretion, the latter providing the main strength for the cells. The coating lined the bottoms and walls of all cells, even shallow peripheral cells that had not produced adults, though in some cases the upper few mm near the rim of these cells lacked it, suggesting that these had recently been heightened by adding carton, but had not yet been coated.

Eggs were attached to the wall of the cell just above the bottom, and always in the uppermost angle of the cell, so that they hung downward nearly parallel to the flat cell bottoms. This position indicates that the queens faced upward on the comb while ovipositing.

Larvae about to pupate spin a silken cocoon completely lining the cell, including the bottom. This lining was distinguishable from the film of secretion lining the cells by virtue of its fibrous texture, greater strength, whiter color, and by its presence only in cells that contained meconia. The silk lining was relatively tough, and with care the entire cocoon, with the meconium at the bottom, could be removed intact from a cell.

The caps of the cocoons were set 2–6 mm below the rims of the cells, were slightly domed, and were translucent at the edges, grading to opaque white in the center. After the cocoon is completed the adults add scattered streaks and blotches of carton to the cap.

After the adult ecloses from a cell, the only treatment the cell receives is to have the cap trimmed away. The walls of the cell are not lowered, nor are the meconia removed, before the cell receives another egg.

No droplets of stored nectar were found in any of the cells of either nest.

Discussion

Though much detail is lacking from Araujo's description of the nest of *C. angustior* (Araujo, 1951), and Dücke's (1910) description of the nest of *C. apicipennis* is even less useful, a few points of comparison with that of *C. weyrauchi* are possible and seem worth making.

The most striking differences pertain to the envelope. While in *C. weyrauchi* there is a wide space separating comb and envelope, Araujo (1951) makes it clear that *C. angustior* starts the envelope by elevating the outer walls of the peripheral cells of the comb, so that the forms of the cells are visible on the sides of the covered nest.

The two species also differ with respect to the nest entrance, that of *C. angustior* protruding somewhat, while that of *C. weyrauchi* is flat.

Though Araujo (1951) states that the envelope of his nest of *C. angustior* contains numerous 'windows' of transparent secretion, he is not clear on their size or nature. He states that they are "perfectly reminiscent" of those

in the nest of *Metapolybia cingulata*. In that species the 'windows' are tiny and are incorporated as the envelope is being built. There is no film of secretion added later to the surface of the envelope. In *C. weyrauchi*, on the other hand, the windows are much larger and are made by the removal of carton from the inside of the film after the envelope is complete. It is not possible to be certain from Araujo's description whether the 'windows' and envelope of *C. angustior* are more like *Metapolybia cingulata* or *C. weyrauchi*, and he does not mention the existence of a surface film of secretion.

Finally, Ducke (1910) states that the nest of *C. apicipennis* seen by him had been enlarged, as indicated by irregularities in the outline of the envelope. On the other hand, neither nest of *C. weyrauchi* showed any evidence of having been enlarged, even though the larger one had evidently housed its colony for nearly a full normal developmental cycle. If *C. weyrauchi*, indeed, does not enlarge its nests once they are built, it is one of few species of New World polybiines not to do so.

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EFFECTIVENESS OF NATIVE PARASITES AGAINST *AGROMYZA*
FRONTELLA (RONDANI) (DIPTERA: AGROMYZIDAE),
AN INTRODUCED PEST OF ALFALFA

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Abstract.—Fourteen species of native parasites of the alfalfa blotch leafminer, *Agromyza frontella* (Rondani), an introduced European pest, were recovered in the northeastern USA. Two additional species were recovered by cooperators in Canada. This complex of native parasites is poorly synchronized with the first 2 generations of the host, which may therefore reach economic injury levels; however, it gives satisfactory control of the next 3 generations. Season-long parasitism averaged 36%, but only 2% of the host puparia were parasitized. European host puparia collected in 1976-77 and shipped to the USDA quarantine facility at Newark produced 7 parasite species with a combined parasitism of 25.5%. All 7 species have been introduced in the USA.

The alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani), is a European species first reported in North America in Massachusetts in 1968 (Miller and Jensen, 1970). It has since spread throughout the northeastern states (Hendrickson and Barth, 1978a) and into the adjoining Canadian provinces (Bereza, 1977). In North America, ABL is frequently an economic pest, though populations in Europe are usually held at low levels, with rare, localized outbreaks (Bollow, 1955).

We therefore surveyed the native North American parasites of ABL to determine their effectiveness and their phenology in relation to the host. Such information was useful in selecting parasite species from a large European complex, studied by personnel at the USDA European Parasite Laboratory, Paris, France, for possible introduction into the USA. The order, family, and identifier of species mentioned in this paper are presented in Table 1.

Sampling techniques.—Samples of 50 mined alfalfa leaflets, that is, leaflets visibly mined by any of the 3 agromyzid species present on alfalfa in the survey area (*Agromyza frontella*, *Liriomyza trifoliarum*, and *Liriomyza trifolii*) were collected randomly each week without regard for host species, instar, or condition of host from early May through November 1975 from each of 7 fields (1 at Newark, Del., 3 near Oxford, Pa., and 3 near Rancocas, N.J.). Collections were not made if the alfalfa was less than 12.7 cm (5 in.) high or bad weather interfered. The same procedure was followed in 1976 and 1977 except that in these years an additional field was surveyed in the

Table 1. Order, family, and identifier of species mentioned in this paper.

Species
HYMENOPTERA: BRACONIDAE
<i>Dacnusa dryas</i> (Nixon) ^a
<i>Dapsilarthra balteata</i> (Thomson) ^d
<i>Opius duresaeui</i> Fischer ^a
HYMENOPTERA: EULOPHIDAE
<i>Achrysocharella Formosa</i> (Westwood) ^c
<i>Chrysocharis clarkae</i> Yoshimoto ^e
<i>Chrysocharis giraulti</i> Yoshimoto ^e
<i>Chrysocharis punctifacies</i> Delucchi ^e
<i>Closterocerus cinctipennis</i> Ashmead ^b
<i>Closterocerus tricinctus</i> (Ashmead) ^b
<i>Closterocerus utahensis</i> Crawford ^b
<i>Diaulinopsis callichroma</i> Crawford ^f
<i>Diglyphus begini</i> (Ashmead) ^e
<i>Diglyphus intermedius</i> (Girault) ^b
<i>Diglyphus pulchripes</i> (Crawford) ^b
<i>Diglyphus websteri</i> (Crawford) ^f
<i>Phygadeuon minio</i> (Walker) ^e
<i>Zagrammosoma multilineatum</i> (Ashmead) ^b
HYMENOPTERA: PTEROMALIDAE
<i>Cyrtogaster</i> sp. ^e
<i>Halticoptera circulus</i> (Walker) ^e
<i>Halticoptera laevigata</i> Thomson ^e
<i>Miscogaster hortensis</i> Walker ^e
<i>Miscogaster maculata</i> Walker ^e
DIPTERA: AGROMYZIDAE
<i>Agromyza frontella</i> (Rondani) ^e
<i>Liriomyza trifoliarum</i> Spencer ^e
<i>Liriomyza trifolii</i> (Burgess) ^e

Identified by:

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^f R. M. Hendrickson, Jr.

Newark, Del., area. Also, collections were made weekly, from mid-April through July, and thereafter at 2-week intervals. However, if the abundance of leaflets containing mining larvae or *Liriomyza trifoliarum* puparia (the other 2 species pupate in the soil rather than in the leaflet) was low, the sample consisted of the number that could be collected in each field in 20 minutes. In the collections over the 3 years, ABL larvae were more abun-

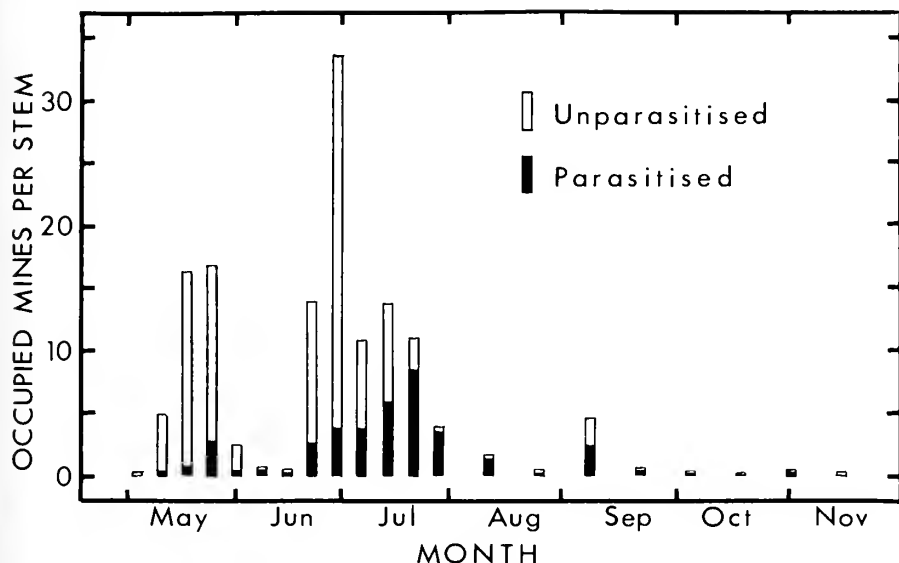


Fig. 1. Ratio of unparasitized to parasitized alfalfa blotch leafminer larvae related to number of occupied mines per stem for 1977. Larvae were collected on alfalfa at 2 fields in Newark, Del., 3 fields near Rancocas, N.J., and 3 fields near Oxford, Pa.

dant than larvae or puparia of *Liriomyza* spp. by ca. 9:1. In addition, we removed 20 stems from each field to determine the number of occupied and unoccupied mines per stem in 1977.

Some host characteristics.—There were 5 generations per year of ABL in the study area. Alfalfa is commonly cut 3 times each season in our area, the last time early in September, and a generation of ABL preceded each cutting. Then the alfalfa continues to grow until the end of November, so there is a period of nearly 3 months during which a 4th and possibly a 5th generation of the ABL can be produced. That these generations do occur was indicated by the presence of some active larvae and adult flies in the field up to the end of November. Pupating larvae of the 5th generation then emerged as adults in late April or early May of the following year. The major peak in population occurred at the time of the 2nd generation when 70+ mines per stem were sometimes encountered (Fig. 1).

Native parasite complex.—A total of 13,551 leaflets containing ABL larvae was placed in 5.08 cm (2 in.) diameter, tightly-sealed plastic petri dishes (one leaf per dish) with moistened filter paper on the bottom to maintain humidity. (So only a single host larva could be confined in each petri dish, any supernumerary insects were removed from the leaflet.) The petri dishes

Table 2. Parasite species and numbers reared from 13,351 alfalfa blotch leafminers collected in Delaware, southern New Jersey, and southeastern Pennsylvania in 1975-77.

Species	Recovered from		Total no.
	Larval stage	Pupal stage	
<i>Diglyphus intermedius</i>	x		1323
<i>Diglyphus pulchripes</i>	x		344
<i>Pnigalio minio</i>	x		152
<i>Diadlinopsis callichroma</i>	x		123
<i>Closterocerus tricinatus</i>	x		78
<i>Chrysocharis clarkae</i>	x	x	65
<i>Closterocerus cinctipennis</i>	x		58
<i>Achrysocharella formosa</i>	x		43
<i>Diglyphus websteri</i>	x		29
<i>Chrysocharis giraulti</i>	x	x	15
<i>Zagrammosoma multilineatum</i>	x		5
<i>Closterocerus utahensis</i>	x		2
<i>Halticoptera laevigata</i>		x	2
<i>Halticoptera circulus</i>		x	1
Unidentifiable ^a			69
	Total		2309

^a Adults were damaged or lost, or larvae were in diapause.

were then maintained at $20^{\circ}\text{C} \pm 1.1^{\circ}$ ($68^{\circ}\text{F} \pm 2^{\circ}$) with 14/24 h photophase. After 6 weeks, emerged parasite species were removed and identified. Initial recoveries were identified by authorities (see Table 1); subsequent recoveries were determined by comparison with identified specimens. Species recovered and numbers are listed in Table 2. Two species of parasites recovered from ABL from eastern Ottawa, Ontario, but not recovered by us in the USA, were the larval parasite *Diglyphus begini* and the larval-pupal parasite *Cyrtogaster* sp. (J. C. Guppy, pers. com.). *Diglyphus begini* was also recovered from ABL at St. Hyacinthe, Quebec (M. Guibord, pers. com.).

There was no emergence of either parasites or ABL from 52% of the mined leaflets. This was probably the result of many factors: early instars killed by probing (without oviposition) by the most abundant parasite, *Diglyphus intermedius* (Hendrickson and Barth, 1978b); overcrowding in the leaflet; host diapause; disease; predators; weather and other physical factors; insecticides; and possible deficiencies in our emergence technique.

At the peak of host larval populations in the 1st generation, an average of 11% of the larvae were parasitized (total live forms). The average was 16% in the 2nd generation. Parasites appeared 2-3 weeks too late in the spring to be effective against the 1st generation of ABL, and too few were present to control the 2nd host generation, when 70+ mines per stem were

Table 3. Parasite species and numbers reared from 33,573 alfalfa blotch leafminer puparia collected in Europe in 1976–1977 by personnel from the USDA European Parasite Laboratory, Paris, France. Parasites emerged in the quarantine facility at the USDA Beneficial Insects Research Laboratory, Newark, Delaware.

Species	No.	% of total parasites
<i>Chrysocharis punctifacies</i>	1656	42
<i>Dacnusa dryas</i>	1614	41
<i>Miscogaster maculata</i> , <i>M. hortensis</i>	571	15
<i>Opius dureseai</i>	47	1
<i>Halticoptera circulus</i>	26	<1
<i>Dapsilarthra balteata</i>	6	<1
Total	3920	

sometimes encountered. During the remaining 3 generations, the average parasitism was 55%, and the host populations remained well below the economic threshold. (A tentative economic threshold of 21% of the leaflets mined by a single larva has been established by R. A. Byers, pers. com.). Combined season-long parasitism was 36% (based on total emerged live forms; numbers of live forms varied for each host generation).

Of the 14 native species recovered from ABL, only 4 species emerged from ABL puparia (Table 2). These species emerged from 1.9% of the 4284 collected hosts which formed puparia.

Origin of the native parasite complex.—A likely explanation for the ABL parasites is adaptation from native agromyzids found on alfalfa. Therefore, petri dishes were set up as before, for 1566 leaflets containing larvae or puparia of *Liriomyza trifoliarum* or larvae of *Liriomyza trifolii* (the latter species pupates in the soil rather than the leaflet). All but 2 of the 14 parasite species recovered from ABL were also recovered from *Liriomyza* spp. The species not recovered were *Zagrammosoma multilineatum* and *Closterocerus utahensis*, which together accounted for only 0.3% of the parasitism of ABL. Possibly with more extensive surveys, these 2 species would also be recovered from *Liriomyza* spp.

We found that *Liriomyza* spp. on alfalfa are under excellent biological control. Season-long parasitism averaged ca. 63%. The complex of native parasites of ABL is therefore probably phenologically associated with that of *Liriomyza* spp.

European survey.—The USDA European Parasite Laboratory, Paris, France, provided us with 33,573 ABL puparia collected from France, Denmark, West Germany, Austria, Switzerland, and Liechtenstein in 1976–77. Parasites or ABL adults emerged from ca. ½ the puparia. Seven parasite species (Table 3) emerged from these collections, all of which have been

released in the USA with additional numbers shipped to us as adults. Parasitism of the pupal stage averaged 25.5%.

We therefore believe the introduction of parasite species capable of increasing parasitism of the pupal stage by 20–25% would reduce ABL to the extremely low population levels found in Europe. The most desirable species for establishment in the USA are *Chrysocharis punctifacies* and *Dacnusa dryas*, which together accounted for 83% of the parasites emerging from European puparia. These species have been established in Delaware (Hendrickson, 1978).

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POSSIBLE PHYLOGENETIC SIGNIFICANCE OF COMPLEX
HAIRS IN BEES AND ANTS

U. N. Lanham

Abstract.—If both larval and adult stages are taken into account, then ants and bees are the only major groups of aculeate Hymenoptera in which complex hairs are abundant. The possible phylogenetic significance of this is discussed.

The first serious attempt at constructing a phylogeny of the higher aculeate Hymenoptera was that of Börner (1919). In it he grouped the bees, scolioid wasps, and ants in a category (the Haplocnemata) which is contrasted with the vespid, pompilid, and sphecoid wasps (Diplocnemata). This scheme has been discussed and rejected by Bischoff (p. 546) and Malyshev (p. 255). The modern conception is that the Apoidea are little modified descendants of the Sphecidae, so closely related that both can be included in a single superfamily (Bohart & Menke, p. 31). Börner, however, has made a considerable contribution to the array of characters available to discriminate higher categories, among them the strigil of the hind leg which, while it establishes his major categories, also provides a useful means of distinguishing apoids and sphecids (Lanham 1960, and Bohart & Menke 1976:27.)

The main difficulty with the concept that bees are essentially sphecoid wasps that have converted from a predatory to a pollen-gathering mode of existence is that intermediate steps have not been found either in morphology or behavior, nor do behavioral patterns of our presently living forms provide material for demonstrating transition stages. If, on the other hand one takes, as a heuristic device, the theory that bees are closely related to ants, then a multitude of possibilities are opened up. Also, one is led into new ways of looking into problems of morphology or behavior. It is not the purpose of this paper to outline a route or routes by which a bee-ant transition could be made, but rather to look at a morphological character whose distribution among the major higher groups of Hymenoptera has been neglected, namely the compound hairs which are generally thought to be characteristic only of the Apoidea (Saunders 1880:202, and most modern textbooks).

All adult bees that I have examined carefully possess at least a few compound (branched, or denticulate) hairs. Bees have in addition other types of complex hairs, such as the spirally twisted hairs in the pollen-transporting brush of the megachilids, or the spatulate hairs on the abdominal terga of some anthophorids, for example *Svastra*.

Rayment (1935:251) notes that compound hairs are present in mutillids, and Brothers (1975:495) assigns the additional "scolioid" families Eotillidae, Typhoctidae and Anthoboscidae to the list of aculeates with such hairs.

Brothers, on the basis of his sample of the ants, assigned to the formicids the character state "simple hairs." It was news to me to find that it has long been known to myrmecologists that adult ants possess complex hair types, including compound hairs. Creighton's key (1950) to North American ants mentions *Acanthomyops plumipilosis* and a species of *Triglyphothrix* as having branched hairs. In a key to the genera of ants of the world Wheeler (1922) mentions a variety of hair types in adult ants: clavate, spatulate, hooked, and denticulate (in mellitology, the last would be called obscurely compound). Ants with these hairs appear to represent scattered species or genera.

If one takes a larger view of the ants, taking into account the larvae, then the ants are not far behind the bees in having bizarre hair structure. About 90% of the genera of ants have quite hairy larvae (nearly all other aculeates have larvae with at best a few bristles). G. C. and J. Wheeler (1976) classify the hairs in nearly 30 categories, using such terms as denticulate, uncinata, anchor-shaped, branched, bifid, or clawlike. In this array, 20 types are compound, in the terminology of bee taxonomy. Data are not presented in such a way as to make a good estimate, but perhaps half the genera of ants, including at least some species of the primitive Australian *Myrmecia*, have larvae with compound hairs.

The Wheelers regard these elaborate larval hairs as adaptations for life in a communal chamber, with the hairs holding them above the substrate, providing insulation and preventing desiccation by producing a dead air space, keeping the brood together by clumping, or helping the larvae cling to vertical surfaces. Probably the only other aculeate Hymenoptera with communal brood chambers (larvae not in individual cells) are a few genera of bees. The most interesting of these on theoretical grounds are the allopine bees, which nest in hollow twigs, have hairy larvae, and in at least one species, have compound (denticulate) hairs (Michener 1977). I am aware of no speculations concerning the function of complex hair types in adult ants.

If one assumes that the presence of compound (or in broader terms, highly modified) hairs in both bees and ants indicates a close phylogenetic relationship, he is of course faced with the difficulty that in ants it is mainly the larvae that have such hairs, while in bees they are found almost exclusively in the adults. One also has to make a judgment concerning the numerous, and so far as known at present, haphazard occurrence of such hairs in adult ants.

Probably the key question is this: are compound hairs easy to originate

de novo in the evolutionary process, or does the establishment of this character require special conditions that are rarely met with.

A significant fact bearing on the question of whether complex hairs are easy to come by is that, so far as I can determine, the hairs are invariably simple among the pompilid, vespid, sphecid, scoliid, and tiphid wasps, which total approximately 15,000 species. Among the thousands of modes of life to be found in these wasps, one would expect that some species would encounter situations in which there would be adaptive value for compound hairs. Those of bees are of use in trapping pollen grains, although on many parts of the body they may also contribute to the density and resilience of the furry coat, affecting such properties as insulation or resistance to abrasion. Some of the vespid wasps gather pollen for their young, but none of these have compound hairs.

It will be assumed here, for purposes of discussion, that compound hairs are difficult to achieve in the evolutionary process, requiring the assembly of a large number of genes into a stable and long-lasting complex. Such complexes then come under the control of a single suppressor or switch gene. Variability of this gene is subjected to selection pressure, establishing alleles which determine whether or not the complex expresses itself, or modulating its expression with respect to body region or stage in life cycle.

Thus, the genetic aspects of our problem come down to this, that the gene complex for a given character, such as the morphology of a single-celled hair, may be multigenic, and may require a long period of time as well as long-lasting and unusually favorable environmental conditions for the assembly of this gene complex. But the addition of a suppressor (switch or control) gene can obscure this situation, making the character act in many ways as if it were based on a single gene. Without direct genetic experimentation, one can only make a judgment on the basis of the distribution of the character within the taxonomic framework. T. D. A. Cockerell early in his career published a few notes on bee phylogeny, but never pursued the matter in print. That he was long interested in basic aspects of the problem is indicated in a paper by himself and Louise Ireland (1933): "... there is increasing proof that the genes for many characters lie latent for long periods, so that similar structures appear in different branches of the same family or order. It may of course be debated whether these reappearances are due to entirely new developments or have a common origin somewhere else in the ancestral germ plasm, or whether they are due to a sort of orthogenesis. It is not necessary to assume that every case may be developed in the same way, but among bees, at any rate, the evidence for germinal continuity and latency seems rather convincing."

Applying the concept of latency to the present problem, one could speculate that the sphecsids and other groups without compound hairs have an

evolutionary background without gene complexes for such structures, and that favorable circumstances for their establishment never arose. The ants and bees both have a background that did include such complexes for producing varied hair types. If one assumes that the modulating capabilities of the suppressor gene make it possible to transfer the expression from larval to adult stage, or adult to larval, there is considerable room for speculative maneuver. Adult ants would be widely infiltrated with suppressed genetic complexes for varied hair types, which surface only here and there, while expression is characteristic of most larvae. In bees the situation is the other way around, with apparently all adults expressing the character, even if only in very rudimentary form. The allodapine bees, which have hairy larvae, are probably still too poorly known to make any judgement as to the extent to which complex hair types are present.

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BOOK REVIEW

George Ordish. *The Year of the Ant*. 139 p. 1978. Charles Scribner's Sons. New York. \$9.95.

This is a delightful description of the ants and their social system, explaining their role in the ecosystem and their ability to survive for millions of years. The explanation of the system, that was able to overcome potential disasters, such as fire, floods, DDT and dependence on slavery and drug addiction, is masterfully presented and of interest not only to the expert myrmecologist, but also to the layman. The author writes with an appealing sense of humor that pervades this volume and provides a real treat. Ants, as well as other social insects, have fascinated man since biblical time. Ants probably originated in North America wherefrom they spread to South America and to Eurasia over the land bridges that once connected the continents. The ant colony is often described as a successful Marxist system, in which each ant gives according to its ability and receives according to its need. However, ants in a colony are not merely part of an automatic machine. There is some free will, as ants enjoy some leisure, such as occasional sunning. Individual ants are capable of learning, and they make choices. The very limited scale of such activities can easily be overridden by the need of the colony and control is exercised by chemical secretions. The author describes this with scientific accuracy by presenting the life cycle of an individual wood ant of a colony. The story begins in March and the star performer is from a monogynous nest, situated in the woods in a clearing in the Adirondack Mountains. Nearby is another, older nest that is polygynous. The behavior of ants in both nests, their contact with aphids, care of eggs, dangerous mites and even more dangerous staphylinid beetle invasions that result in drug addiction, the emergence of males and mating, robber ants, loss of the queen and transformation of the worker into a queen, and finally the fight with another queen and the decapitation of the "heroine" are chronologically presented, from March till October of "the year of the ant." The chapters are aptly illustrated by Clarke Hutton. There is a bibliography of books and original articles and a subject index.

This book can be read profitably not only as an introduction to social insects, but also by the specialist. The book can be recommended to students, teachers, and research scientists, as well as for general academic libraries, public libraries and high schools. The good quality of the print and paper in a book costing less than \$10.00 might also be mentioned. In short, the author succeeded in providing a book not only for entomologists but

also for a more general audience, that merits reading by all interested in biology. Several copies should be made available in the libraries of high schools and academic institutions.

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BOOK REVIEW

Tabanini of Thailand above the Isthmus of Kra (Diptera: Tabanidae). John J. S. Burton. 165 pp. 1978. Entomological Reprint Specialists, Los Angeles, California. \$15.00.

Female Tabanini are well known blood suckers, whereas the males mostly feed upon honeydew and on juices of flowers. These flies play an important role in spreading agents of certain infectious diseases such as Surra to livestock—especially virulent in equine species. Tabanini also play a role in the spread of tularemia to man. The biological diversity and economic importance of gadflies has been the subject of many scientific papers. Although the oriental tabanid fauna is unusually rich, it remained the least known up to now. Therefore this excellent study is very important and it is useful not only insofar as the tabanid fauna of Thailand and southeast Asia is concerned, but also for the whole oriental zoogeographic region.

In twelve chapters the author presents detailed information about the economic importance of gadflies, collections made in Indochina, superspecific taxa of Tabanini with reference to Thailand, the species concept, field procedures, descriptions of species, and a key to females. The interesting and detailed study of the tribe Tabanini comprises 81 species, of which 31 are described as new and 24 nominal taxa are newly synonymized. For many species lectotypes are given and some new generic combinations are proposed. The study is illustrated with 80 excellent figures. The last chapter deals with other species involved or implicated in the transmission of disease agents in the Indochina area.

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A BRIEF REVIEW OF THE GENUS *CICINDELA* OF ARGENTINA
(COLEOPTERA: CICINDELIDAE)

William D. Sumlin, III

Abstract.—The genus *Cicindela* L. (*sensu* W. Horn) of Argentina is briefly reviewed. Thirty-four taxa are discussed and known ranges are given. A key to the species is presented. Four new species and one new subspecies are described and figured. Three of the new species (*C. halophila*, *C. siccalacicola* and *C. hirsutifrons*) share the same type locality: 24 mi. S. Recreo, Cordoba Province. The fourth new species (*C. stamatoivi*) is described from Tucuman. *C. drakei latifascia* n. ssp. is described from Termas de Rio Hondo, Santiago del Estero Province.

Introduction

The genus *Cicindela* of Argentina has not been adequately reviewed. It has been presented in the form of checklists by Horn (1905), Bruch (1910), Horn (1915, 1926), Blackwelder (1946) and Rivalier (1954).

The latter author incorporated a study of male genitalia into his work and split the genus into several "genera." Following Rivalier's work, Vidal Sarmiento (1966) gave a detailed account of the male genitalia for many of the species. Although that work was detailed, with respect to the males of the species reviewed, it failed to incorporate a key or deal with females.

The present work treats 34 taxa with five being described as new. I have endeavored to treat all specific and subspecific taxa contained in Horn's (1926) definition of the genus *Cicindela* of Argentina with the exception of *C. cribrata* Brullé. I feel that Rivalier's (1969) placement of *cribrata* into *Pentacomia* Bates is correct. I do not, however, subscribe to his splitting up the New World *Cicindela* in 1954. Rivalier's "genera" are herein treated as subgenera.

Many of the species treated in the present work are quite rare in collections and as a result some were only represented by one or two specimens. In some cases Argentine specimens were not available for study and specimens from other countries had to be utilized. Two species (*C. argentinica* Mandl and *C. obsoletesignata* W. Horn) were unavailable for study which necessitated culling key data from their original descriptions.

All characters used in the key below are easily seen and interpreted. To facilitate usage, with respect to the terminology of the elytral maculation, users are directed to Figure 1 which deals with lunule nomenclature.

Key to Species of *Cicindela* of Argentina

- | | |
|---|-------------------------------|
| 1. Elytra immaculate | 2 |
| – Elytra with some degree of maculation | 4 |
| 2. Dorsal color dark reddish brown | <i>rufoaenea</i> |
| – Dorsal color black | 3 |
| 3. Labrum 3 toothed | <i>obsoletesignata</i> |
| – Labrum 4 or 5 toothed | <i>morio</i> |
| 4. Genae glabrous | 5 |
| – Genae setose | 13 |
| 5. Maculation very wide, covering much of elytral surface | 6 |
| – Maculation thin or consisting of small spots | 7 |
| 6. Basal half of elytra sparsely covered with white setae | <i>eugeni</i> |
| – Basal half of elytra without white setae | <i>apiata</i> |
| 7. Elytral apex immaculate | 8 |
| – Elytral apex with maculation | 9 |
| 8. Dorsal color black or dark brown | <i>obscura</i> |
| – Dorsal color green tinged cupreous red | <i>aureola</i> |
| 9. Elytra with distinct subsutural rows of large metallic foveae | 10 |
| – Elytra without distinct subsutural rows of large metallic foveae | 11 |
| 10. Size smaller (8 mm in length) | <i>chlorosticta</i> |
| – Size larger (12 mm in length) | <i>staudingeria</i> |
| 11. Apex of elytra rounded (see Fig. 2a) | <i>argentata</i> ¹ |
| – Apex of elytra angular (see Fig. 2b) | 12 |
| 12. Humeral lunule broken—consisting of two small spots | <i>misella</i> ² |
| – Humeral lunule complete and unbroken | <i>stamatovi</i> n. sp. |
| 13. Pigment (ground color) contacting lateral edges of elytra | 14 |
| – Pigment not contacting lateral edges of elytra (i.e., maculated from humeral area to apical suture) | 24 |
| 14. Apex of elytra without microserrations | 15 |
| – Apex of elytra with microserrations | 16 |
| 15. Labrum with a longitudinal black band running through its median | <i>gormazi</i> |
| – Labrum not as above | <i>sinuosa</i> |
| 16. Frons with less than 6 setae | <i>confluentesignata</i> |
| – Frons with more than 6 setae | 17 |
| 17. Labrum with a longitudinal dark band running through its median | <i>chiliensis</i> |
| – Labrum not as above | 18 |

¹ *C. argentinica* (Mandl) will also key out in this couplet. See under Discussion section.

² *Pentacomia cribrata* (Brullé) will also key out in this couplet. It can be separated from *C. misella* Chaudoir by its glabrous undersides. Also, see Rivalier (1969) for further discussion.

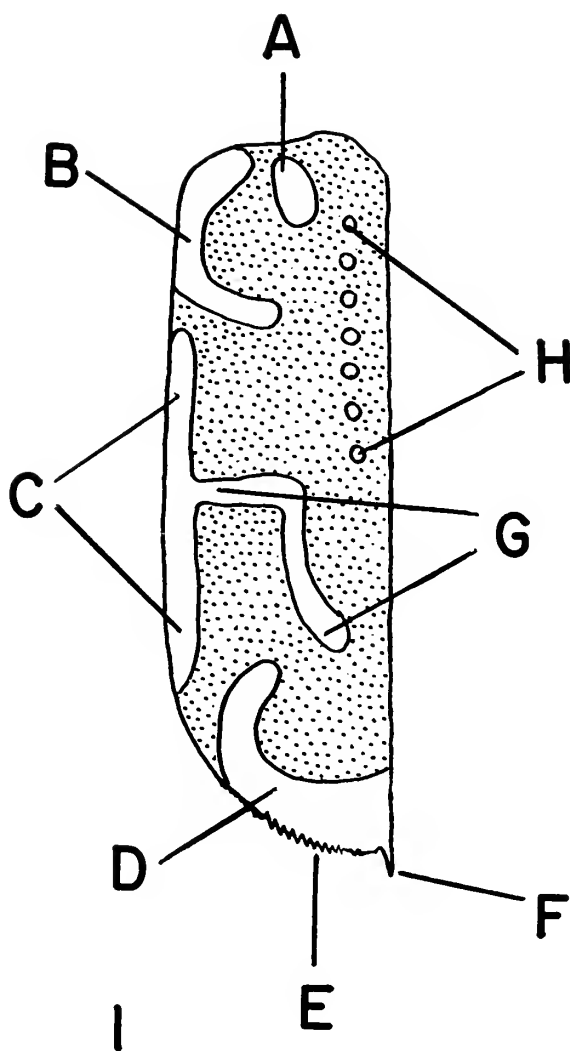


Fig. 1. Left elytron of a hypothetical *Cicindela* species illustrating terminology used in key:
 A) basal dot, B) humeral lunule, C) marginal line, D) apical lunule, E) microserrations, F)
 sutural spine, G) middle band, H) subsutural row of foveae.

- | | |
|---|------------------|
| 18. Labrum with more than 9 subapical setae | <i>mixtula</i> |
| – Labrum with 9 or less subapical setae | 19 |
| 19. Elytral ground color black | <i>melaleuca</i> |
| – Elytral ground color brown or reddish brown | 20 |
| 20. Maculation not contacting medial lateral edge of elytra | <i>ritsemai</i> |
| – Maculation contacting medial lateral edge of elytra | 21 |

- | | | |
|---|----------------------------------|----|
| 21. Marginal line not converging on humeral lunule | <i>drakei drakei</i> | |
| – Marginal line converging on humeral lunule | | 22 |
| 22. Size larger (12 mm in length) | <i>sinuosa</i> | |
| – Size smaller (9 mm in length) | | 23 |
| 23. Head and pronotum dark cupreous red | <i>drakei pseudochiloleuca</i> | |
| – Head and pronotum dark green | <i>drakei latifascia</i> n. ssp. | |
| 24. Frons completely covered from view with white decumbent setae | <i>hirsutifrons</i> n. sp. | |
| – Frons glabrous or with setae but not covered from view | | 25 |
| 25. Elytra dull, reflecting little light | | 26 |
| – Elytra shiny, reflective | | 28 |
| 26. Vertex glabrous | <i>confluentesignata</i> | |
| – Vertex setose | | 27 |
| 27. Antennal scape glabrous (except for subapical sensory setae) | <i>patagonica</i> | |
| – Antennal scape with several white setae (if setae are rubbed off, minute dimples are present) | <i>ramosa</i> | |
| 28. Clypeus glabrous | <i>halophila</i> n. sp. | |
| – Clypeus setose | | 29 |
| 29. Antennal scape glabrous (except for subapical sensory setae) | <i>siccalacicola</i> n. sp. | |
| – Antennal scape with several white setae | <i>nivea</i> | |

In the ensuing section only the new taxa are fully discussed. The remaining species and subspecies are briefly discussed.

The known ranges and collecting data (where available) are presented alphabetically by province. Many of the study specimens are from older collections and carry labels simply stating "Argentina" or "Buenos Aires" or some other province with no other data. For this reason, there are no collecting data provided for several taxa.

The phylogeny of Rivalier (1954), with slight modification, is followed.

Subgenus *Cicindelidia* Rivalier, 1954

Cicindela rufoaenea W. Horn

Cicindela unicolor W. Horn 1892, Deutsche Ent. Zeitschr. p. 86 (preoccupied).

Cicindela rufoaenea W. Horn 1915, in Wytsman, Gen. Ins. Cic. p. 402.

This species is the only representative of the above subgenus known from Argentina. It can be distinguished immediately by its immaculate, red-brown color and testaceous abdomen.

Type locality.—"Argentinisches Hochgebirge."

Range.—Jujuy: 5 km. S. San Pedro, 5-V-64; Salta; Peru; Colombia.

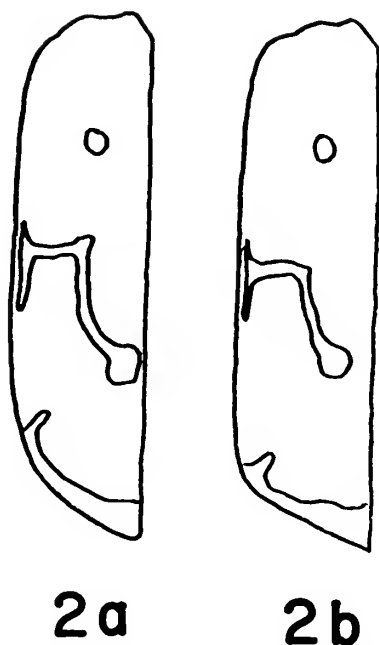


Fig. 2a. Left elytron of *C. argentata* showing a rounded apex. 2b. Left elytron of *C. misella* showing an angular apex.

Subgenus *Brasiella* Rivalier, 1954

Cicindela argentata argentata Fabricius

Cicindela argentata Fabricius 1801, Syst. Eleuth. I, p. 242.

C. argentata, once thought to be a single species, has proven to be a "species swarm." Many of the species within this swarm can only be separated by characters contained within the aedeagus.

Argentine samples of *C. argentata* run from well-marked light-brown individuals to dark-brown or black individuals with broken lunules, seemingly in a random fashion. However, all the samples have several characters in common: truncate labrum, rounded elytral apices and the characteristic *argentata* inner sac of the aedeagus.

Type locality.—"America Meridionali."

Range.—*Buenos Aires*: San Fernando, III-1956; Corral del Cruz, II-1964; *Chaco*; *Cordoba*: V. Dolores, II-1969; *Formosa*: P. Irigoyen, XII-1950; *Jujuy*; *Misiones*; *Salta*: Gen. Ballivian; C. Olleros, I-1958; *San Luis*; *Santa Fe*: Dpto. Garay, III-1950; Gran Guardia, II-1953; *Santiago del Estero*: Cap. Aeropuerto, II-1961; *Tucuman*: Tucuman, I-51; *Brazil*; *Venezuela*; *Colombia*; *Paraguay*.

Cicindela argentata semicircumscripta Mandl

Cicindela argentata semicircumscripta Mandl 1958, Ent. Nachr. Österr. Schweiz. Ent., 10 (2), p. 23.

This subspecies can be separated from the nominate form by its greenish elytra and long marginal line.

Type locality.—"Santiago del Estero, El Pinto."

Range.—*Santiago del Estero*: El Pinto, XI-1962; Rio Saladillo, 29-XII-1975; Suncho Corral, 28-XII-1975; Paraguay.

Cicindela argentinica (Mandl)

Brasiliella (sic) *argentinica* Mandl 1963, Ent. Arb. Mus. G. Frey, 14, p. 583.

No specimens of this species were available for study. In reading Mandl's description and studying his accompanying figures, one quickly learns that it is quite difficult to separate *C. argentinica* from *C. argentata*. According to the description, *argentinica* has an almost cylindrical pronotum and an apical lunule that extends a good distance up the suture.

Type locality.—"Argentine, Rio Salado, Icano."

Range.—At present, known only from the type locality.

Cicindela obscurella obscurella Klug

Cicindela obscurella Klug 1829, Preis-Verz. Ins. Mus. Berlin, p. 3.

This species can be identified by its lack of an apical lunule and its rounded, slightly produced labrum. Some specimens possess a spot representing the humeral lunule.

Type locality.—"Sud-Brasilien."

Range.—*Buenos Aires*: Corral del Cruz, II-1964; *Cordoba*; *Tucuman*: Tucuman, 7-II-1908; Brazil; Uruguay.

Cicindela aureola aureola Klug

Cicindela aureola Klug 1834, Jahrb. Ins. I, p. 35.

C. aureola can be separated immediately from the rest of the *argentata* complex by its green tinged cupreous red color. Apparently it is sexually dimorphic, with respect to the shape of the labrum; males possess short labra while the female's is produced.

Type locality.—"Südlichen Brasilien."

Range.—*Jujuy*; *Salta*; *Tucuman*; Paraguay; Brazil.

Cicindela misella misella Chaudoir

Cicindela misella Chaudoir 1854, Bull. Soc. Imp. Nat. Moscou, 27, p. 121.

For years this species was thought to be confined to Central America and northern South America. Vidal Sarmiento (1966) proved its existence in Argentina. It can be separated from *argentata* by its angular elytral apices and characteristic inner sac.

Type locality.—"Colombie."

Range.—Jujuy; Salta; Venezuela; Colombia north to Guatemala.

Cicindela stamatovi n. sp.

(Fig. 3a, b)

Head.—Labrum white with a narrow, dark anterior border, equipped with a single row of subapical setae (8 setae), slightly produced, rounded, single-toothed; first four antennal segments metallic cupreous with green reflections; scape with a single subapical seta; second, third and fourth segments with a few erect white setae; clypeus, frons and genae glabrous, finely rugose and striate; vertex glabrous (except for supraorbital sensory setae).

Thorax.—Pronotum with sparse decumbent setae on lateral margins and disc, finely rugose, narrowed posteriorly; pro-, meso- and medial metasternum glabrous; remainder of thorax with sparse erect setae.

Abdomen.—Lateral edges of venter with sparse covering of decumbent setae, glabrous medially.

Elytra.—Both sexes, nearly parallel-sided although slightly wider from basal third to apical fourth, then more or less oblique from apical sixth to apex; both sexes with small sutural spines, microsculptured apical margins and shallow green punctae; elytral surface granulate; maculation complete, humeral lunule long and slender, descending nearly to apical half, remainder of lunules of the *argentata* type.

Color.—Head, dorsal and lateral portions of thorax metallic cupreous with green reflections; ventral thorax and abdomen metallic green to dull, dark green; elytra cupreous with metallic green punctae.

Size.—Male, 6.4 mm length, 2.2 mm width; female, 6.5 mm length, 2.4 mm width.

Type locality.—Tucuman, Argentina.

Holotype.—Male. Tucuman, II-50, Arg.

Allotype.—Female. Same data as holotype. Holotype and allotype to the American Museum of Natural History, New York City, New York.

Etymology.—I take pleasure in naming this species after Dr. John Stamatov, who kindly submitted the specimens for study.

Diagnosis.—*C. stamatovi* appears to be closest to *C. misella* in the Argentine fauna. It can be separated from *misella* by its produced labrum and

complete humeral lunules. *C. stamatovi* is apparently the only species in the "argentata complex" with a complete humeral lunule.

Cicindela chlorosticta Kollar
(Figs. 3, 4)

Cicindela chlorosticta Kollar 1836, Ann. Wiener Mus. Naturg., 1 (2), p. 332.

No Argentine representatives of this species were available for study. Key characters were drawn from specimens collected in Brazil.

Type locality.—"Brasiliae Provincia Ypanema."

Range.—Jujuj; Brazil.

Cicindela staudingeria W. Horn

Cicindela staudingeri W. Horn 1892, Deut. Ent. Zeitschr., p. 368 (preoccupied).

Cicindela chlorosticta staudingeria W. Horn 1915, in Wytsman, Gen. Ins. Cic., p. 404.

No Argentine representatives of this species were available for study. Key characters were drawn from Brazilian specimens. It differs from *chlorosticta* by its larger size and coloration. Most specimens are a brilliant cupreous color.

Type locality.—"Sao Paulo."

Range.—Argentina; Brazil.

Cicindela obsoletesignata W. Horn

Cicindela obsoletesignata W. Horn 1895, Deutsche Ent. Zeitschr., p. 91.

No specimens of this species were available for study. It is apparently quite rare in collections. Horn (1895) compares it with *C. hemichrysea* Chevrolat but the coloration is similar to *C. morio* Klug.

Type locality.—"St. Catharina."

Range.—Santa Fe = Chaco Santafecino; Brazil.

Subgenus *Cylindera* Westwood, 1831

Cicindela confluentesignata W. Horn

Cicindela confluens W. Horn 1893, Deutsche Ent. Zeitschr., p. 197 (preoccupied).

Cicindela confluentesignata W. Horn 1915, in Wytsman, Gen. Ins. Cic., p. 407.

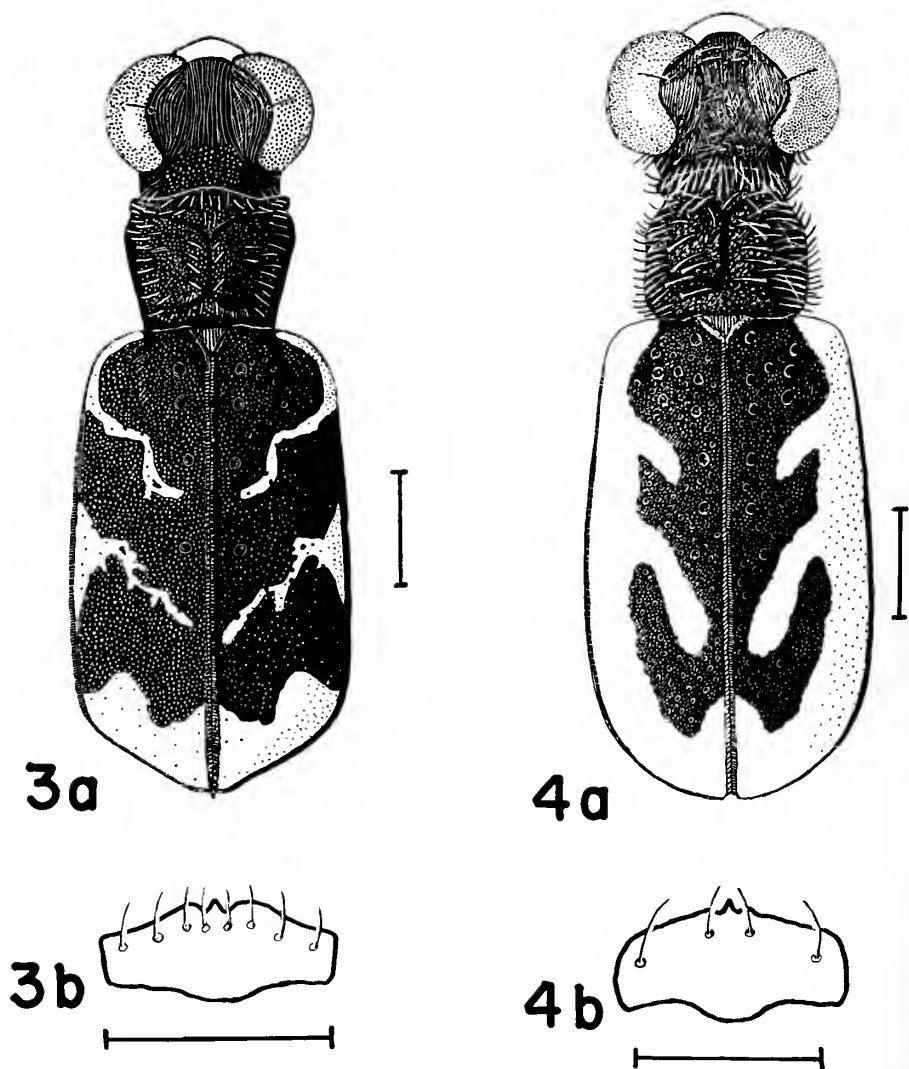


Fig. 3a. Dorsal aspect of holotype male of *C. stamatovi* n. sp. 3b. Dorsal aspect of labrum of *C. stamatovi* n. sp. Fig. 4a. Dorsal aspect of male *C. halophila* n. sp. 4b. Dorsal aspect of labrum of *C. halophila* n. sp. All scale lines indicate 1 mm.

One Argentine representative of this species was available for study. Key characters were drawn from that exemplar and from Paraguayan specimens. It is a distinctive species, bronze-black in color, with many elytral foveae.
Type locality.—"Minas Geraes."

Range.—*Entre Rios*: Pronunciamiento, XII-1961; *Formosa, Santiago del Estero*; Brazil; Paraguay.

Cicindela eugeni Castelnau

Cicindela eugeni Castelnau 1835, Etudes Ent., pt. 1, fasc. 1, p. 36.

A distinctive species not treated by Rivalier (1954). Known by its confluent maculation and setose elytra.

Type locality.—"Cordova."

Range.—*Cordoba, Santiago del Estero*: 50 km. NE. Santiago del Estero, 16-XII-1971.

Cicindela halophila n. sp.

(Fig. 4a, b)

Head.—Labrum white with a single row of subapical setae (4–5 setae), slightly produced, single toothed; antennal scape metallic green with cupreous reflections, equipped with a single subapical seta; third antennal segment with 6–8 erect white setae; clypeus glabrous, metallic green; genae with sparse covering of white decumbent setae; frons and vertex glabrous (except for two erect supraorbital setae, per side, near front of eye and one over eye), finely wrinkled.

Thorax.—Pronotum with sparse covering of white decumbent setae (extreme medial area glabrous), finely rugose; proepisternum, prosternum, propimeron, procoxa, mesepimeron, mesocoxa, metaepisternum, anterior edge of metasternum and lateral edge of metacoxa with covering of white decumbent setae; mesepisternum with decumbent setae along ventral edge, mesosternum glabrous.

Abdomen.—Lateral edges of venter with a covering of white decumbent setae, glabrous medially; posterior two, visible, abdominal segments red-testaceous.

Elytra.—Male and female, nearly parallel-sided although slightly wider from basal third to apical third, then gradually rounded from apical fifth to apex; males without sutural spines; females with a small, slightly retracted spine; both sexes with microserate apical margins and shallow punctae; maculation consists of a broad marginal band running from the humeral area along the lateral edge to the apex and thence to the suture at the apical fifth; humeral lunule enters disc obliquely; middle band begins descent into disc at apical half and descends nearly to apical fifth.

Color.—Anterior portion of head metallic green with cupreous reflections; remainder of head cupreous metallic (except for genae, which are metallic green); pronotum metallic red cupreous with metallic green sulci; lateral portions of thorax metallic cupreous; undersides all metallic cupreous with

green tinges; abdomen dull green metallic with last two segments red-testaceous; elytra bright red-brown with green punctae throughout pigmented portion.

Size.—Male, 7.5 to 7.9 mm in length, 2.5 to 2.8 mm in width; female, 8.1 to 8.5 mm in length, 2.8 to 3.0 mm in width.

Type locality.—Argentina, Cordoba Province, 24 mi. S. Recreo.

Holotype.—Male. 24 mi. S. of Recreo, Cordoba, R. A., II-9-51, Salt Flat, Ross and Michelbacher collectors.

Allotype.—Female. Same data as holotype.

Paratypes.—4 males, 3 females (one female damaged), same data as holotype; 2 males, La Colina B. A., Buenos Aires, Arg., 12-9-1938, Carl J. Drake; 1 female, Estrella, Chaco, Prg., XII-43, N:1. Holotype, allotype and three paratypes to the California Academy of Sciences, San Francisco, California; three paratypes to the National Museum of Natural History, Washington, D.C.; one paratype to the American Museum of Natural History, New York City, New York. The remaining paratypes are in the author's collection.

Etymology.—Name derived from the Greek for salt-lover, alluding to the new species' occurrence on a salt playa.

Diagnosis.—*C. halophila* n. sp. appears to be closest to *C. eugeni*. It can be separated from that species by slightly different markings, color, elytral lustre, and absence of setae on the anterior basal half of the elytra, and the presence of setae on the genae.

Cicindela morio morio Klug

Cicindela morio Klug 1834, Jahrb. Ins. I, p. 16.

No Argentine representatives were available for study. Key data were obtained from Brazilian specimens.

Type locality.—"Brasilien."

Range.—N. Argentina; Brazil.

Cicindela sinuosa Brullé

Cicindela sinuosa Brullé 1837, Voyage Orbigny, Ins. Col., p. 8.

A single female specimen referable to this species, labeled "Misiones," was used for key data. Brullé compared *sinuosa* with *C. trisignata* Dejean and his description seems to maintain that comparison. The illustration by Horn (1938, Table 84, Fig. 11), however, bears little resemblance to Brullé's description or the specimen currently at hand. The study specimen (badly damaged) resembles a broadly marked *C. mixtula* W. Horn.

Type locality.—"Corrientes."

Range.—Corrientes; Entre Rios; Misiones.

Cicindela mixtula mixtula W. Horn

Cicindela mixta W. Horn 1892, Deutsche Ent. Zeitschr., p. 215. (preoccupied).

Cicindela mixtula W. Horn 1915, in Wytsman, Gen. Ins. Cic., p. 409.

Apparently a fairly common species in Argentina—at least it is frequently collected.

Type locality.—"Tarija (Bolivia)."

Range.—Catamarca: S. Maria, 19-I-1945; Formosa: Desmonte, XII-1950; Jujuy: Quemado, III-1926; Mendoza; Salta: La Termes, 17-X-1975; San Juan: Retamito, 17-III-1907; San Luis: Kahuel Mopa, I-1964; Tucuman: Cadillal, 4-XII-1975; Tucuman, 20-XI-1913, 2-XI-1916, 30-XI-1919; Vipos, IV-1960; Bolivia.

Cicindela drakei drakei W. Horn

Cicindela drakei W. Horn 1892, Deutsche Ent. Zeitschr., p. 85.

This species is easily confused with *C. melaleuca reedi* W. Horn but, may be distinguished by its brown color, instead of the black of *reedi*.

Type locality.—"Mendoza."

Range.—Mendoza; Salta; Tucuman.

Cicindela drakei pseudochiloleuca W. Horn

Cicindela drakei pseudochiloleuca W. Horn 1908, Ent. Wochenblatt, 25, p. 209.

Subspecies *pseudochiloleuca* is differentiated by its smaller size and the shape and extent of the lunules; it has a marginal line that is connected to the humeral lunule, something not found in the nominate form. Also, *pseudochiloleuca* possess a rather diffuse, indistinct descending portion of the middle band.

Type locality.—"Tukuman (Argentinien)."

Range.—Tucuman.

Cicindela drakei latifascia n. ssp.

(Fig. 5)

Similar in most respects to subspecies *pseudochiloleuca* but differing in that the new subspecies possesses a green head and pronotum (as opposed to the cupreous color of the former) and the lunules are much wider and more distinct.

Type locality.—Terma-Rio Hondo, Santiago del Estero Province, Argentina.

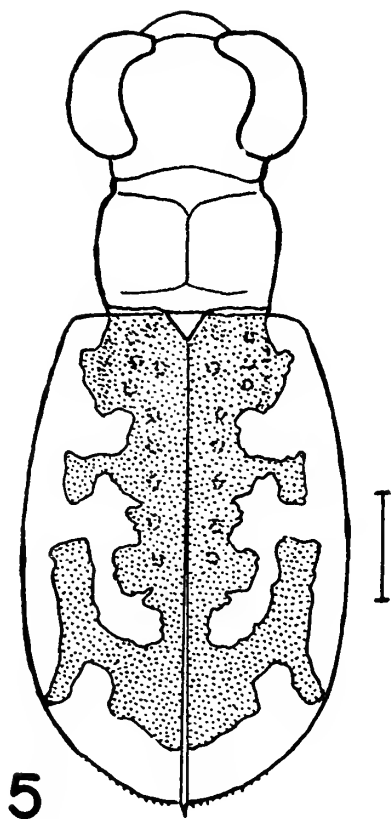


Fig. 5. Dorsal aspect of holotype male of *C. drakei latifascia* n. ssp. Scale line indicates 1 mm.

Holotype.—Male. Argentina, Sgo. Estero, Termas de Rio Hondo, 30-XII-1975, R. M. Bohart. Holotype to the University of California, Davis collection.

Etymology.—Name derived from the Latin *lata* (wide) and *fascia* (mark).

Diagnosis.—The new subspecies can be easily separated from the nominate subspecies and *pseudochiloleuca* by its green head and pronotum and the very wide markings. After studying long series of *pseudochiloleuca* (to which *latifascia* appears closest) from Tucuman, I found no tendency toward wide lunules or green coloration of the head or pronotum.

Cicindela melaleuca melaleuca Dejean

Cicindela melaleuca Dejean 1831, Spec. Col. V, p. 238.

C. melaleuca is a distinctive black species with a humeral lunule that normally comes in contact with the anterior-most part of the middle band.

Type locality.—"Buenos-Ayres."

Range.—Buenos Aires: San Fernando, XII-1962; Guamini, II-1964; La Colina, 9-XII-1938; Mendoza; Patagonia.

Cicindela melaleuca reedi W. Horn

Cicindela reedi W. Horn 1895, Deutsche Ent. Zeitschr., p. 88.

This subspecies has been placed under *C. drakei* by several workers including Horn (1926). Horn (1938), however, placed it with *C. melaleuca*, where I feel it justly belongs.

The differences in genitalia and external morphologies between *C. drakei* and *C. melaleuca* are slight. When large samples are examined from their respective ranges it may be found that the two species are actually one—a brown form with its melanic counterpart.

Type locality.—"Patagonia."

Range.—Patagonia.

Cicindela siccalacicola n. sp.

(Fig. 6a, b)

Head.—Labrum white with a narrow dark anterior border, equipped with a single row of subapical setae (6–9 setae), slightly produced, rounded, single toothed; first four antennal segments metallic cupreous with green reflections; scape with a single subapical seta; second, third and fourth segments with several erect setae; clypeus and genae with sparse covering of partially erect white setae; frons and vertex with sparse covering of partially erect to erect white setae.

Thorax.—Pronotum sparsely covered with partially erect white setae, finely rugose; pro- and mesosternum glabrous, remainder of thorax with sparse, erect setae.

Abdomen.—Lateral edges of venter with a covering of decumbent setae, glabrous medially.

Elytra.—Male, nearly parallel-sided although slightly wider from basal fourth to apical third, then gradually rounded from apical fourth to apex; female, markedly widened from basal third to apical third, then gradually rounded to apex; both sexes equipped with small sutural spines, microserate apical margins and shallow, green punctae; maculation complete, marginal line broad, connected with humeral lunule and outer edge of apical lunule; humeral lunule a knob pointing laterally; middle band elbowed at center of elytral disc, descending to edge of apical third; apical lunule large, comma-shaped.

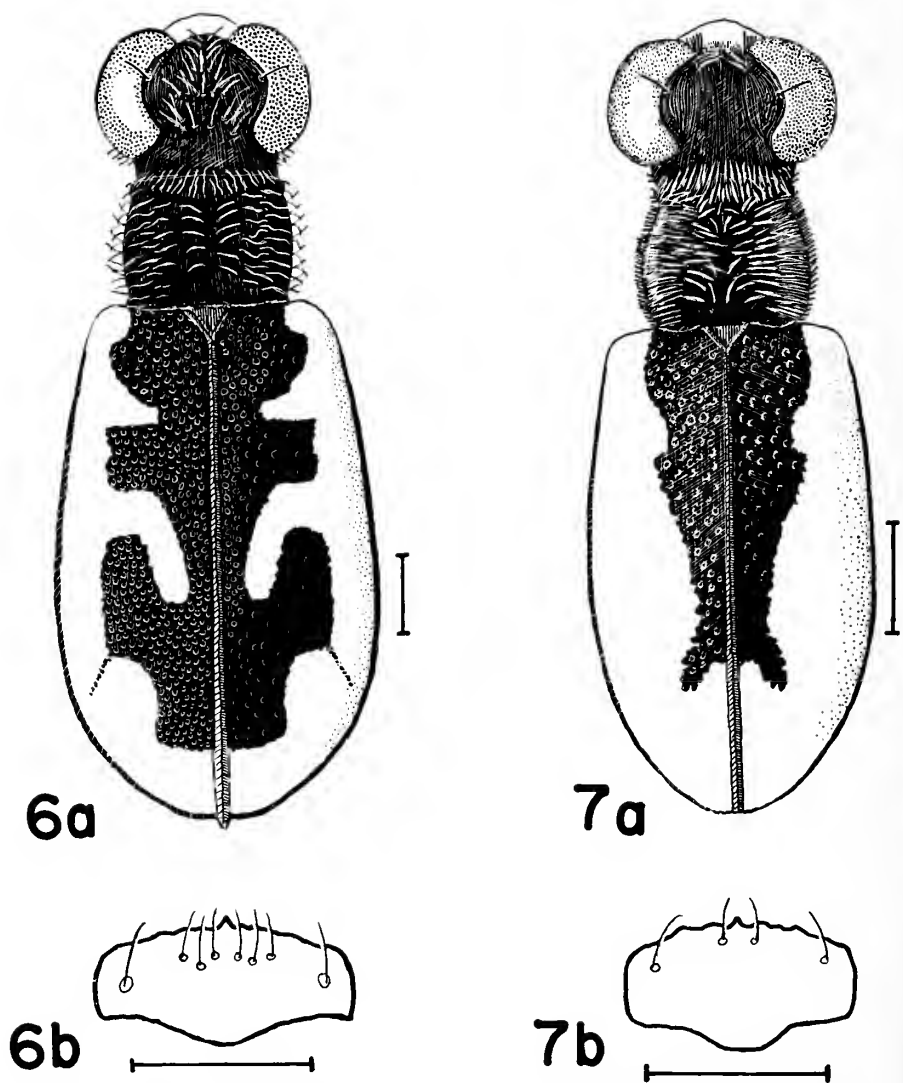


Fig. 6a. Dorsal aspect of male *C. siccalacicola* n. sp. 6b. Dorsal aspect of labrum of *C. siccalacicola* n. sp. Fig. 7a. Dorsal aspect of holotype male of *C. hirsutifrons* n. sp. 7b. Dorsal aspect of labrum of *C. hirsutifrons* n. sp. All scale lines indicate 1 mm.

Color.—Head predominately metallic cupreous with green reflections; pronotum cupreous with green reflections, medial sulcus metallic green; lateral portions of thorax metallic cupreous; ventral portions of thorax blue-green metallic with cupreous reflections; abdomen dark brown with green

reflections, cupreous laterally; elytra dark red-brown covered with metallic green punctae.

Size.—Male, 10.5 mm length, 3.5 mm width; female, 11.5 mm length, 4.5 mm width.

Type locality.—24 mi. S of Recreo, Cordoba Province, Republic of Argentina.

Holotype.—Male. 24 mi. S Recreo, Cordoba, R. A., II-9-51, Salt Flat, Ross and Michelbacher collectors.

Allotype.—Female. Same data as holotype.

Paratypes.—16 males, 12 females same data as holotype.

Holotype, allotype and 17 paratypes to the California Academy of Sciences, San Francisco, California; one paratype each to the National Museum of Natural History, Washington, D.C., and the American Museum of Natural History, New York City, New York. The remaining paratypes are in the author's collection.

Etymology.—The name of the new species is derived from the latin *sicca* (dry), *lacuna* (lake), and *incola* (dweller).

Diagnosis.—This species is apparently not closely related to any other known from Argentina. With its unusual maculation pattern and near-glossy elytra it is quite distinct.

Discussion.—The range of this species apparently extends into Buenos Aires Province as I have before me a female (not in the type series) collected at La Colina. This specimen is larger (13.5 mm in length) than the females of the Cordoba series and is dark green in color. The status of this population is unknown.

Cicindela ritsemai W. Horn

Cicindela ritsemae W. Horn 1895, Notes Leyd. Mus., 17, p. 15.

Cicindela ritsemai W. Horn 1915, in Wytzman, Gen. Ins. Cic., p. 409.

A distinctive little species, apparently rare in collections. It slightly resembles *C. drakei pseudochiloleuca*, but can be separated from that taxon by the marginal line that fails to contact the elytral lateral margins.

Type locality.—"Argentiniae (Provincia Catamarca)."

Range.—Catamarca; Cordoba; Santiago del Estero: Termas de Rio Hondo, XII-30-1975; Suncho Corral, XII-28-1975; Tucuman: Cadillal, XII-4-1975.

Cicindela gormazi Reed

Cicindela gormazi Reed 1871, Ent. Mo. Mag., 8, p. 76.

No Argentine specimens were available for study. Key data were drawn from Chilean specimens.

Type locality.—"Chile merid."

Range.—Chubut; Patagonia; Chile.

Cicindela chiliensis Audouin & Brullé

Cicindela chiliensis Audouin & Brullé 1839, Arch. Mus. Hist. Nat., 1, p. 133.

No Argentine representatives of this species were available for study. Key data were extracted from Chilean specimens.

Type locality.—"Chili."

Range.—Chubut; Patagonia; Chile.

Cicindela patagonica patagonica Brullé

Cicindela patagonica Brullé 1837, Voyage Orbigny, Ins. Col., p. 7.

This species is readily confused with *C. ramosa* Brullé. They are easily separated by the lack or presence of setae on the scape of the antenna.

Nominate *patagonica* is a brown tiger beetle with fairly thin markings.

Type locality.—"Rio Negro (Patagonie)."

Range.—Buenos Aires; Patagonia.

Cicindela patagonica cherubim Chevrolat

Cicindela cherubim Chevrolat 1858, Ann. Soc. Ent. France, ser. 3, 6, p. 315.

Similar to the nominate form except that the markings are much wider, the ground color is blue and the elytra are expanded laterally.

Type locality.—"Montivideo."

Range.—Buenos Aires; Uruguay.

Cicindela patagonica bergiana W. Horn

Cicindela patagonica var. *bergiana* W. Horn 1895, Anal. Mus. Nac. Buenos Aires, 4, p. 174.

Identical with the preceding form except that the ground color is brown.

Type locality.—"Montevideo."

Range.—Buenos Aires; Uruguay.

Cicindela apiata apiata Dejean

Cicindela apiata Dejean 1825, Spec. Col., 1, p. 86.

Apparently the most common member of the genus is Argentina—at least it is collected more often than other species.

Type locality.—"meridionale du Bresil."

Range.—*Buenos Aires*: Buenos Aires, II-1936, XII-1940; La Colina, 29-XI-1938; R. Sauce Grande, 23-II-1968; San Fernando, I-1962, Tandileofu, 23-II-1968; Veronica, I-1922; *Cordoba*: 22 km. S. Alta Gracia, 18-XI-1975; Capilla del Monte; Cosquin, 1-9-III-1920; *Entre Rios*: Concordia; 4 km. N. Va. San Jose, 15-XI-1973; *Mendoza*; *San Luis*; *Santiago del Estero*: Termas de Rio Hondo, 30-XII-1975; *Tucuman*; Brazil, Paraguay; Uruguay.

Cicindela ramosa Brullé

Cicindela ramosa Brullé 1837, Voyage Orbigny, Ins. Col., p. 7.

A distinctive species with very broad markings. It is usually green in color.

Type locality.—"baie de San-Blas."

Range.—*Buenos Aires*: Buenos Aires, XII-1938; Guamini, II-1964; Lag. Las Tunas, 4-IX-1961; *Catamarca*: Andaleala, XI-1945; *Patagonia*; Uruguay.

Cicindela nivea nivea Kirby

Cicindela nivea Kirby 1818, Trans. Linn. Soc. London, 12, p. 376.

No Argentine representatives of this subspecies were available for study. Key data were drawn from Brazilian specimens.

It is a large Argentine *Cicindela* (13 mm in length) with markings so broad they completely cover the elytra with white in most examples.

Type locality.—"Brasilia."

Range.—*Buenos Aires*; *Misiones*; *Entre Rios*; Brazil; Uruguay.

Cicindela nivea orbignyi Guérin-Ménéville

Cicindela intricata Brullé 1837, Voyage Orbigny, Ins. Col., p. 7 (preoccupied).

Cicindela orbignyi Guérin-Ménéville 1839, Rev. Zool., p. 296.

Differentiated from the nominate form by the increased amount of pigmentation on the elytra.

Type locality.—"la Patagonie."

Range.—*Buenos Aires*: Necochea, II-1927, XII-1963; *Patagonia*; Uruguay.

Cicindela hirsutifrons n. sp.

(Fig. 7a, b)

Head.—Labrum testaceous with a narrow border of dark brown on anterior edge (labral color in a degreased specimen would probably be white),

equipped with a single row of subapical setae (4 setae), produced, rounded, single toothed; first four antennal segments green-metallic with cupreous reflections, scape with a single subapical seta, segments 3 and 4 nearly covered with broad, white decumbent setae; segment 2 glabrous; clypeus and genae with dense covering of wide, white decumbent setae; frons and anterior edge of vertex completely covered with wide, decumbent setae; remainder of vertex glabrous (except for supraorbital sensory setae); base of mandibles with a sprinkling of decumbent setae.

Thorax.—Pronotum nearly covered with white decumbent setae, disc sparsely setose, finely rugose; proepisternum, proepimeron, procoxa, mesepimeron, socoxa, metaepisternum, anterior edge of metasternum, ventral edge of mesepisternum and lateral edge of metacoxa with dense covering of white decumbent setae; mesosternum glabrous.

Abdomen.—Lateral edges of venter with dense covering of white decumbent setae, sparsely setose medially; posterior two visible, abdominal segments red-testaceous.

Elytra.—Male, nearly parallel-sided, slightly expanded from basal fourth to apical fourth, then gradually rounded to apex; female, unknown; male without sutural spines or microsculptate apical margins, shallow punctae cover surface; maculation consists of a band of white starting at the humerus and running to the suture at the apical fourth gradually widening as it progresses so that over 60% of the elytra are white; middle band, humeral and apical lunules are only hinted at, very confluent type of maculation.

Color.—What can be discerned (due to extreme pilosity) of the anterior portion of the head is metallic green with cupreous reflections; genae metallic cupreous; vertex metallic cupreous with green reflections; pronotum metallic cupreous with medial sulcus metallic green; lateral and ventral portions of thorax metallic cupreous with green tinge; abdomen dark brown with metallic red reflections with last two segments red-testaceous; elytra bright red metallic.

Size.—Male, 8.6 mm in length, 2.5 mm in width; female, unknown.

Type locality.—24 mi. S. Recreo, Cordoba Province, Republic of Argentina.

Holotype.—Male (damaged). 24 mi. S. Recreo, Cordoba, R. A., 9-II-1951; Salt Flat, Ross and Michelbacher collectors. Holotype to the California Academy of Sciences, San Francisco, California.

Etymology.—The new species name is a combination of the latin *hirsuta* (hairy) and *frons* (forehead).

Diagnosis.—*C. hirsutifrons* appears to be closer to *C. nivea* than to any other species in Argentina. It can be separated readily from *nivea* by its smaller size, coloration, extent of pilosity, shape and type of maculation.

Remarks.—Although the holotype is damaged (it appears to have been

struck with the edge of a collecting net); it is nonetheless complete, except for a portion of one antenna.

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REPRODUCTIVE BEHAVIOR OF *EUARESTA BELLA* AND
E. FESTIVA (DIPTERA: TEPHRITIDAE), POTENTIAL
AGENTS FOR THE BIOLOGICAL CONTROL OF
ADVENTIVE NORTH AMERICAN RAGWEEDS
(*AMBROSIA* SPP.) IN EURASIA

S. W. T. Batra

Abstract.—Larvae of *Euaresta bella* (Loew) and *E. festiva* (Loew) destroy seeds of *Ambrosia artemisiifolia* L. and *A. trifida* L., respectively; *E. bella* has been colonized in the USSR for ragweed control. The univoltine adults feed on honeydew and ragweed sap. In Maryland, *E. bella* adults reach peak abundance in mid-August, *E. festiva* a month later. Courtship behavior by both sexes is complex, involving several stereotyped wing movements, proboscis and foot contact, head butting, and male territoriality or lekking. Oviposition occurs in the young female flowers.

Introduction

The native North American ragweeds, *Ambrosia artemisiifolia* L., *A. trifida* L. and *A. psilostachya* DC., have become accidentally established in Eurasia, where they cause increasing agricultural and medical problems (Goeden et al., 1974). *Ambrosia artemisiifolia* and *A. trifida* are abundant in the northeastern United States, producing about 90% of the hayfever-causing late summer pollen to which about 4% of the population is sensitive (Dickerson and Sweet, 1971). These rapidly growing annuals are among the most important weeds in row crops, pastures, ornamentals and small fruits in the United States (Danielson et al., 1965). *A. artemisiifolia* and *A. trifida* have become established and troublesome in the southwestern USSR (Shutova, 1970), which is climatically similar to the eastern United States. The study of the bionomics of insects that attack ragweed in the northeastern United States was initiated by the author in 1976, and several species were shipped to the USSR. These included 425 adult *Euaresta bella* (Loew), which were colonized in 1977 at Sochi (O. V. Kovalev, personal comm.).

Euresta bella is a small univoltine tephritid that occurs throughout the United States on *A. artemisiifolia*, its sole host (Foote, 1965; Wasbauer, 1972). In Ohio adults are found from mid-June to late September; reproduction begins in August; the larvae develop and overwinter in the seeds, destroying 1-15%; and pupation occurs in spring (B. A. Foote, 1965; in litt. 1977). *Euaresta festiva* (Loew) is a larger univoltine species that attacks only *A. trifida* in the eastern and midwestern states. In Ohio adults appear

in July; larvae destroy 2–25% of the seeds, where they overwinter; and pupation occurs in spring (B. A. Foote, 1965; in litt., 1977). The seed-feeding habit of larvae of these two tephritids contrasts with that of the larvae of *Euarestoides acutangulus* (Thomson), which destroy the staminate flowers of *Ambrosia* spp. (Piper, 1976).

Field and cage observations of *Euaresta bella* and *E. festiva* were made between 1976 and 1978 at the USDA Agricultural Research Center, Beltsville, Maryland. Caged adult flies were kept in a rearing room at 16L:8D hr. photoperiod, at about 25°C, or were kept in a greenhouse at ambient day-length at about 27–30°C. They were provided with vigorous potted host plants, water droplets, and food (4:1 sucrose/autolyzed yeast extract in water). Individual flies lived as long as two weeks.

E. bella adults began to appear in the field at Beltsville in mid-July, the females at that time being noticeably slender, with translucent abdomens; at this time the host plants were not yet blooming. The adult population of this insect reached a maximum in mid-August, when the male and female flowers of *A. artemisiifolia* began to bloom, and abdomens of female flies at this time were swollen and opaque. The fly population subsequently declined rapidly as most ragweed plants set seed, although male flowers continued to produce abundant pollen. By the end of August, *E. bella* adults were scarce. However, *E. festiva* reached its peak abundance in mid-September on the later-blooming *A. trifida*.

Both *E. bella* and *E. festiva* were relatively most active and phototactic during the late afternoon. They flew poorly, *E. bella* hopping only a few centimeters from leaf to leaf; *E. festiva* flying erratically for one or two meters to adjacent plants. Dispersive ability of individual flies is apparently slight, as in *Urophora jaceana* (Hering), which did not cross a two meter wide cart track to host plants on the other side (Varley, 1946).

Adult *E. bella* and *E. festiva* often licked ragweed leaves. Additionally, *E. bella* licked dew, honeydew of aphids and leafhoppers, the foam of cerco-pid larvae on ragweed stems, sap oozing from damaged leaves, and the sucrose-yeast-water mixture. A droplet of food sometimes was repeatedly regurgitated and reingested by both sexes, behavior resembling nectar-whipping by bees, which reduces the water content. Honeydew and dew are often eaten by other tephritids (Christenson and Foote, 1960; Bateman, 1972).

Courtship and Territoriality

The courtship behavior of *E. bella* and *E. festiva* is variable and complex (Table 1), involving stereotyped movement of the conspicuously patterned wings, visual orientation, wing and abdomen vibration, proboscis and foot contact, head butting, and lekking or male territoriality. As in *Valentibulla*

Table 1. Major courtship behavior patterns of *E. bella* and *E. festiva*. C, common, R, rare, —, not seen.

	<i>E. bella</i>		<i>E. festiva</i>	
	♂	♀	♂	♀
(1) Visual orientation	C	C	C	C
(2) Alternate wing waving with vibration	C	C	C	C
(3) Both wings extended horizontally	R	—	—	—
(4) Both wings extended with proboscis extended	C	C Front legs also extended	—	—
(5) Both wings extended with head butting	C	C	R	—
(6) Tapping with front feet	—	R	R	—
(7) Rapid flicks of both wings simultaneously	C	—	C With proboscis extension	—
(8) Territoriality (lekking)	C	—	C	—
(9) Following female, abdomen curved	R	—	C	—
(10) Following female, wings flattened against abdomen	—	—	C	—

(Wangberg, 1978), both sexes play active roles in courtship and the sequence of courtship displays is frequently interrupted and resumed at various stages.

Visual orientation by both sexes toward conspecific flies of both sexes (Table 1: item 1), and to other small insects was common. Orienting flies turned to face these insects as they moved about, and grooming was occasionally begun by flies that had been watching conspecifics or other insects that were grooming themselves. Orientation is common in many tephritids (Tauber and Toschi, 1965; Piper, 1976; Berube, 1978; Wangberg, 1978) and in *Drosophila* (Spieth, 1974).

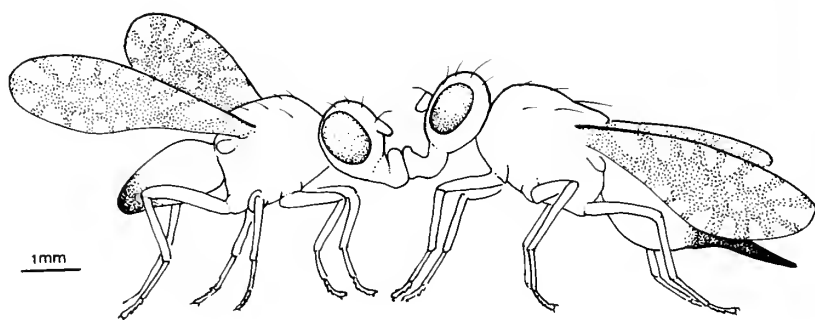
During orientation, random walking, and (in females) while mating, both species of *Euaresta* often slowly waved alternate wings. A slight vibration of the extended, vertical wing was sometimes seen, and side-stepping may occur (Table 1: 2). Occasionally an *E. bella* male or female faced another fly of either sex while waving alternate wings (Fig. 1); the other fly responded by synchronous ipsilateral wing waving. Similar behavior occurs in *Euarestoides acutangulus* (Piper, 1976), *Tephritis dilacerata* Loew (Berube,



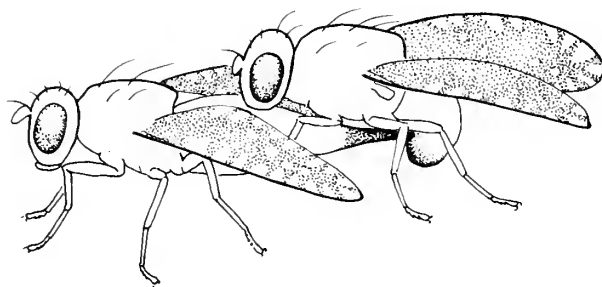
Figs. 1-4. *Euaresta bella* on *Ambrosia artemisiifolia*. 1. Female waving alternate wings while approaching a resting male. 2. Male performing the spread-winged display to an intruding male, in defense of its territory. 3 and 4. Females ovipositing through the floral involucre.

1978) and *T. stigmatica* (Coquillett) (Tauber and Toschi, 1965); it may be a general species recognition signal in *E. bella*.

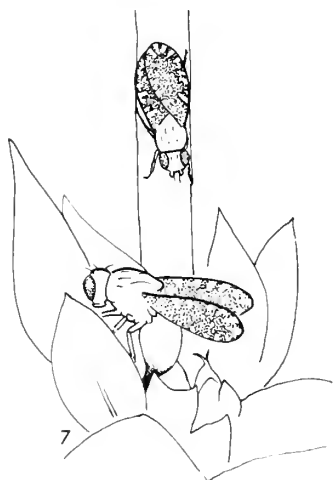
A behavior pattern peculiar to both sexes (but usually seen in males) of *E. bella* is a simultaneous horizontal spreading of both wings (Table 1: 3-5). The vertically tilted wings are spread out for several seconds while the fly turns toward another fly of either sex or another small insect. A conspecific fly may respond by similarly spreading its wings while facing the instigator (Fig. 2); the abdomen may vibrate. After approaching, one of the



5



6



7



8

Figs. 5-8. *Euaresta festiva* and *E. bella*, as drawn from color slides. 5. Proboscis contact or 'kissing' by male and female *E. festiva*. 6. Copulation of *E. festiva*. 7. Female *E. festiva* ovipositing, as male watches in precopulatory attitude. 8. Copulation of *E. bella*.

flies may butt the other with its head (Table 1: 5), or both flies may make contact with each other's proboscis (Table 1: 4); a female may extend her front feet in addition to her proboscis. Unlike *Drosophila* (Spieth, 1974), and *E. festiva*, this 'kissing' in *E. bella* is not only used for courtship, but appears to be related to territoriality, because one of the flies (usually not the initiator) abruptly leaves the area after kissing, butting, or wing spreading displays. Proboscis extension is usually initiated by males, but occasionally females approach other females in this way (20 ♂: 3 ♀-initiated). Butting and chasing other *E. bella* (including a mating pair) or other insects (gnats, small Hemiptera, beetles, ants), was performed by both sexes (17 ♂: 6 ♀). Nonreceptive females thus deterred male advances. Male *E. festiva*, before following females, extended their probosces to make contact with those of females (Fig. 5) in conjunction with abdomen vibration and wing flicking, as part of the courtship.

Rapid, repeated, simultaneous flicking (10/sec.) of both wings is characteristic only of males in both *E. bella* and *E. festiva* (Table 1: 7). Male *E. festiva* flicked their wings while orienting toward both sexes, while mating, and occasionally before the spread-winged display.

Lekking or male territoriality by male *E. festiva* and *E. bella* was common (Table 1: 8). This behavior pattern also occurs in male *Rhagoletis* (Christenson and Foote, 1960), *U. jaceana* (Varley, 1946), and *Valentibulla* spp. (Wangberg, 1978). Territories of male *E. bella*, on one or two leaves of the host, were about 7–10 cm sq., and appeared to be occupied by individual males for only a few hours (males were not marked for recognition); the same areas were usually not used the next day. The larger territories of male *E. festiva* are about 1 m sq.; males returned to their territories after flying away when they were disturbed by the observer. Male *E. bella* drove other insect species and other males from their territories by butting them or running at them with their probosces and wings extended. Wandering females were displayed to when they entered or approached male territories. The aggressiveness of males toward each other and toward nonreceptive females may be advantageous to the species, by aiding dispersal and subsequent oviposition in a larger number of plants. Female-female aggression, as in *Dacus dorsalis* Hendel (Christenson and Foote, 1960) also helps to disperse the population and avoid multiple ovipositions in the small *Ambrosia* fruits.

Male *E. festiva*, more often than male *E. bella*, were seen closely following females; their abdomens were ventrally curved (Table 1: 9, 10). These males kept their wings folded closely, one above the other, above their abdomens while following or observing females (Fig. 7); they waited 2–4 cm away while females completed probing or ovipositing in flowers before they moved closer and attempted to copulate from the rear. Although mating in

E. festiva is associated with oviposition, as in *T. dilacerata* (Berube, 1978), ovipositing females of *E. bella* were not noticeably attractive to males.

Copulation and Oviposition

Mating in *E. festiva* occurred between 14:20 and 18:00 EDT; two copulations lasted 57 and 58 minutes (Fig. 6). Couples walked or flew and both sexes occasionally flicked their wings. In *E. bella*, mating occurred between 8:00 and 17:00 EDT, with most copulations about 16:00, when the flies generally were most active. Fifteen copulations lasted 20–60 minutes each (Fig. 8). Females walked, fed, performed the spread-winged display, and butted at nearby flies while mating; males occasionally flicked their wings.

Fecund females of *E. bella* and *E. festiva* wandered over the leaves and stems of their hosts, but female flowers in the upper half of the plants were most attractive to ovipositing flies. Before ovipositing or probing the flowers with the ovipositor, flies walked about over the flowers, and occasionally contacted them with their probosces. *E. festiva* characteristically stood above the female flowers while probing or ovipositing (Fig. 7). The ovipositor was inserted for 10 to 60 seconds; the shorter times being apparently probes, since eggs were not subsequently found, although the sides of the flowers' involucres and ovaries had been slit (brown slit marks, 0.3 to 0.7 mm long). In *E. bella*, such probing by the ovipositor slits numerous floral ovaries, causing necrosis and sterility of about 30% of the flowers that were probed, even when eggs were not laid. As described by Foote (1965), eggs of *E. bella* are partially inserted into young flowers at the edges of flower clusters or deposited on their surfaces; larvae then enter and totally destroy the developing seeds; eggs of *E. festiva* are placed inside the involucre against the seed coat (B. A. Foote, in litt.). During oviposition, *E. bella* typically penetrated flowers through the involucre from the side (Figs. 3 and 4), often with a rocking motion as the ovipositor was inserted. Probing and oviposition was seen between 13:30 and 17:05 EDT and each lasted 15 to 50 sec. Ovipositing females often probed several flowers in succession; one female probed six flowers in 15 minutes. Females usually groomed themselves after probing each flower.

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ACOUSTIC ATTRACTION OF HERONS BY CRICKETS

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Abstract.—Male crickets of the species *Anurogryllus celerinictus* attract mates after sunset by giving a loud sustained calling song. A predator, the heron, *Florida coerulea* uses this sound to locate its prey. *F. coerulea* was also attracted to a tape recorded song of *A. celerinictus*.

It was first suggested by Lutz (1924) that predators such as frogs, lizards and birds likely hear and respond to insect sounds. Walker (1964) experimentally demonstrated that domestic cats can acoustically locate singing orthopteran prey. Cade (1975) and Soper et al. (1976) reported on dipteran parasites orienting to the sound of their insect prey. Bird predators should be capable of hearing songs of certain Grylloidea (Marler, 1955). Yet, no one has shown that birds locate insect prey by using the prey's sound(s).

In May, 1978, at Ocho Rios, Jamaica I observed an adult little blue heron, (*Florida coerulea*) to orient to a tape-recorded calling song of the fast-calling, short-tailed cricket, *Anurogryllus celerinictus* (Walker). The heron(s) was observed to stalk, catch and eat crickets, at night between the hours of 20:00 and 22:00 EDT. This time period coincides with the crickets' peak acoustical activity (Bell, In Press). Many of the villagers were familiar with these, "dark, cricket-eating sea gulls." During daylight hours the same species of heron fished shallow, slow-moving freshwater streams.

Two Philips tweeters were positioned 5 M apart, magnets down on a flat lawn. Over one speaker, using a Uher 4000 Report L, the recorded calling song of a male *A. celerinictus* was played for 20 min. periods. The second speaker was silent. On one occasion an adult *F. coerulea* was approximately 30 M from the speakers when a recording was begun. Immediately the heron turned toward the speakers. It approached the live speaker, stalking slowly and turning its head from side to side. The heron came within 1 m of the live speaker, and was never closer than 5 m from the silent speaker. After seeing myself and the recorder the heron turned away from both speakers, walked a few steps (1 m), and caught and ate a cricket.

Male *A. celerinictus* call to attract females for the purposes of mating. Being nocturnal singers, and associated with burrows, these crickets escape most daytime predators. However, herons appear to locate these crickets in the dark by orienting to the cricket's song.

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COMMUNITY ECOLOGY AND *PIERIS*—CRUCIFER
COEVOLUTION^{1,2}

F. S. Chew

The association of certain subfamilies of Lepidoptera with certain families of flowering plants whose members are exploited as larval food is well known (e.g. Ehrlich and Raven, 1965; Fraenkel, 1959; Whittaker and Feeny, 1971). Among the Pierinae, for example, larvae of the genus *Pieris* are confined to the Cruciferae, Capparidaceae, and a small number of other plant families whose members contain glucosinolates (mustard oil glucosides; Ettlinger and Kjaer, 1968). A number of glucosinolates, tested under laboratory conditions, appear to mediate specificity in these plant-insect associations by eliciting feeding and oviposition responses from various *Pieris* (e.g. David and Gardiner, 1966; Hovanitz and Chang, 1963) as well as from other crucivorous species (e.g. Thorsteinson, 1953; Tanton, 1965; Hicks, 1974). In addition, allylisoithiocyanate, the volatile hydrolysis product resulting from enzymatic degradation of allylglucosinolate (sinigrin) when crucifer tissues are damaged, acts as an attractant to *Pieris rapae* and some chrysomelid beetles (Blau et al., 1978; Feeny et al., 1970; Matsumoto, 1970). Specific electrophysiological responses of *Pieris brassicae* to individual glucosinolates (Schoonhoven, 1967) and laboratory behavioral tests of insect ability to discriminate among glucosinolates (e.g. Hovanitz and Chang, 1963; Hicks, 1974) suggest that *Pieris* and other crucifer specialists may distinguish among various Cruciferae (and other glucosinolate-bearing taxa) on the basis of this chemical class of more than 70 compounds (Ettlinger and Kjaer, 1968; Rodman, 1978). In this paper I present evidence that *Pieris* preferences among several co-occurring crucifer species in a community are correlated with the presence of specific glucosinolates in these species. These results suggest that by affecting the intensity of *Pieris* herbivory on their allelochemically-similar neighbors, individual crucifer species may influence each other's evolution.

How do *Pieris* choose foodplants among allelochemically-similar taxa in a community? Chew (1974, 1975, 1977) characterized the behavioral and growth responses of a population of *Pieris napi macdunnoughii* to Crucif-

¹ Based on paper contributed to symposium "Components of Host-Plant Utilization in Lepidoptera" (P. Barbosa, organizer) presented at Eastern Branch Meetings, Entomological Society of America, 27 September 1978.

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erae in its montane habitat (Table 1). *P. n. macdunnoughii* responses to the native crucifer taxa in this community comprise three categories: a) a preferred foodplant, *Descurainia richardsonii* (nomenclature follows Weber, 1976) which supports significantly faster larval development to pupation than other native foodplants; b) a group of foodplants which support similar larval growth rates and among which adults and larvae show no consistent preferences, viz., *Arabis drummondii*, *Cardamine cordifolia*, *Draba aurea*, and *Thlaspi montanum*; and c) a crucifer which is unconditionally rejected by both ovipositing adults and feeding larvae—*Erysimum asperum*. The behavioral responses of *P. n. macdunnoughii* adults and larvae to these crucifers are thus consistent with each other: larvae are able to complete larval development on all crucifer species chosen by ovipositing females. In contrast, behavioral and growth responses of *P. n. macdunnoughii* to the naturalized weed *Thlaspi arvense* are inconsistent with each other: females accept *T. arvense* as an oviposition substrate and larvae feed on the plant, but die before completing development. Similar incongruity between female oviposition behavior and larval growth responses has been observed in a variety of Lepidoptera exposed to previously unencountered relatives of their foodplants (e.g. Straatman, 1962; Sevastopulo, 1964; Bowden, 1971). This inconsistency also characterizes the behavioral and growth responses of *Pieris occidentalis*, another native Colorado species, toward *T. arvense*. *P. occidentalis* places significantly fewer eggs on *T. arvense* than on native crucifers (Chew, 1977); however, unlike *P. n. macdunnoughii* avoidance of *Erysimum asperum*, *P. occidentalis* avoidance of *T. arvense* is statistical rather than absolute, with the result that substantial numbers of *Pieris* eggs are placed on this lethal plant. Since *T. arvense* is naturalized to this region, perhaps insufficient time has elapsed for the resolution of this incongruity. Botanical surveys of this region (see Chew, 1977) suggest that *T. arvense* has been abundant in this community for less than 100 years. Given the present pattern of behavior and mortality on *T. arvense*, *P. n. macdunnoughii* and *P. occidentalis* should eventually reject *T. arvense* plants as oviposition sites; alternatively, because females currently oviposit on *T. arvense* and larvae feed on the plant before dying (Chew, 1975), selection may favor any change which permits larvae to develop successfully on this plant.

Examination of the leaf glucosinolate profiles of these crucifer species shows that this community contains three distinct glucosinolate arrays (Table 2). The group of four species (in which *P. n. macdunnoughii* exhibits no consistent preference) is characterized by isopropyl glucosinolate and several biosynthetically related compounds. The unconditionally rejected plant, *Erysimum asperum*, contains methylsulfanylalkyl and methylsulfonylalkyl compounds, which are distinct from other major components of other glucosinolate profiles. Since some plants in this genus and the related

Table 1. Growth and behavioral responses of *Pieris napi macdunnoughii* to crucifer species growing in a montane Colorado community. These species include all locally abundant taxa which contain glucosinolates. Data are summarized from Chew (1974, 1975, 1977).

Crucifer species	Oviposition	Feeding	Growth to pupation
(a) <i>Descurainia richardsonii</i>	Prefer	Prefer	Fastest
(b) <i>Arabis drummondii</i>	Yes	Yes	Yes
<i>Cardamine cordifolia</i>	Yes	Yes	Yes
<i>Draba aurea</i>	Yes	Yes	Yes
<i>Thlaspi montanum</i>	Yes	Yes	Yes
(c) <i>Erysimum asperum</i>	No	No	No
<i>Thlaspi arvense</i> ¹	Yes	Yes	No

¹ Naturalized from Eurasia.

genus *Cheiranthus* contain cardenolides (Hegnauer, 1964) *Erysimum asperum* may be chemically distinctive in this community on that basis as well; however, this species has not been examined for cardenolide content. The third array (with allylglucosinolate as a major component) includes both the preferred foodplant *Descurainia richardsonii* and the naturalized lethal crucifer *Thlaspi arvense*. Unlike the first two glucosinolate arrays, which correspond directly to crucifers in two behavioral-growth response categories, this third array comprises two crucifers whose effects on these *Pieris* are widely divergent.

The correlation of glucosinolate profiles with *Pieris* larval and adult behavior suggests that *P. n. macdunnoughii* distinguish among these crucifers at least partly on the basis of their glucosinolate profiles. In the case of *Erysimum asperum*, lack of information on the possible cardenolide content of this species precludes determination of what allelochemic class(es) mediates rejection of this plant by *Pieris* (Nielsen, 1978). While the possible physiological effects of individual glucosinolates on adapted crucivores such as *Pieris* have only begun to be explored (e.g. Marsh and Rothschild, 1974; Aplin et al., 1975; Blau et al., 1978), *Pieris* behavior towards *T. arvense* suggests that allylglucosinolate is perceived as a signal of suitable larval food. The allyl compound, and other major components of these glucosinolate profiles, are probably not intrinsic indicators of foodplant suitability for larval *Pieris*. Rather, *Pieris* behavior toward specific individual glucosinolates shared by several taxa probably depends on the evolutionary association of those glucosinolates with food resources of a particular quality. For these Colorado *Pieris*, it is likely that the consistent association of allylglucosinolate with the foodplant *Descurainia richardsonii* has been dis-

Table 2. Results of qualitative analysis of crucifer leaves for glucosinolates. Paper and gas-chromatographic methods are outlined by Rodman (1974). Data are summarized from unpublished data of Rodman and Chew.

Crucifer species	Major glucosinolates (aglycone moiety)	Minor glucosino- lates (number only)
I. <i>Arabis drummondii</i> ¹	Isopropyl-, 2-hydroxyisopropyl-, 2-butyl-	5
<i>Cardamine cordifolia</i>	Isopropyl-, 2-hydroxyisopropyl-, 2-butyl-, 1-ethyl-2-hydroxyethyl-	1
<i>Draba aurea</i>	Isopropyl-	2
<i>Thlaspi montanum</i>	Isopropyl-, 2-butyl-, (p)-rhamnopyranosyloxybenzyl-	1
II. <i>Erysimum asperum</i>	3-methylsulfinylpropyl-, 4-methylsulfonylbutyl	0
III. <i>Descurainia richardsonii</i>	Allyl-, 3-butenyl-	5
<i>Thlaspi arvense</i>	Allyl-	2

¹ Roman numerals refer to crucifer arrays described in the text.

rupted by the relatively recent introduction of *Thlaspi arvense* to this community; ovipositing adults may be confusing the lethal *T. arvense* with its allelochemically-similar associate *D. richardsonii*.

These data suggest that variation among members of a single chemical class may be significant in modifying insect behavior toward plants which contain this chemical class (cf. Dethier, 1978). For glucosinolates, variation may occur in two ways. First, biosynthesis of the aglycone moiety of the glucosinolate may vary, giving rise, for example to the hydroxylated compounds found in *Arabis drummondii* and *Cardamine cordifolia*; variation in the number of methylene groups occurs in *Descurainia richardsonii*. These changes probably involve minor modifications of existing biosynthetic pathways (e.g. Chew and Rodman, 1979 and references therein). In this case it is probably significant that electrophysiological work on *Pieris brassicae* shows that the receptors of this crucivore are more sensitive to the glucosinolates tested than to their corresponding isothiocyanates (Schoonhoven, 1967). Alternatively, after biosynthesis, a single glucosinolate may generate different aglycone products upon enzymatic hydrolysis (Benn, 1977). Allylglucosinolate, for example, may give rise to allylisothiocyanate or its isomer allylthiocyanate; allylthiocyanate has been found as the major hydrolysis product of *T. arvense* by others (e.g. Gmelin and Virtanen, 1960) but preliminary tests of *T. arvense* from this montane community reveal

allylthiocyanate as the major product. Feeny and colleagues (Feeny et al., 1970; Feeny, 1977) have shown that allylthiocyanate is much less attractive to crucivorous chrysomelid beetles under field conditions than the corresponding isothiocyanate.

While the variation generated within each crucifer species will be largely constrained by existing biosynthetic pathways (cf. Atsatt and O'Dowd, 1976), the adaptive value of a particular glucosinolate variant in a particular crucifer species depends on its relation to glucosinolates already present in the community (Jones, 1968; Dolinger et al., 1973; Janzen, 1973; Atsatt and O'Dowd, 1976; Cates and Rhoades, 1977; Feeny, 1977, Moore, 1978b). *Pieris* response to a novel compound in the glucosinolate profile of a particular crucifer will thus depend a) on whether it mimics the glucosinolate profile already produced by some other community associate (cf. Macior, 1970); b) on *Pieris* growth responses to species containing that glucosinolate; and c) on whether *Pieris* distinguish the plant containing the new glucosinolate from chemically-similar taxa in the community. To the extent that glucosinolates mediate the responses of *Pieris* towards their foodplants and to the extent that *Pieris* activity imposes differential mortality on different chemical morphs within crucifer populations (Jones, 1971; cf. Moore, 1978a; Morrow and LaMarche, 1978), it seems likely that these crucifer species evolve in relation to each other as well as in relation to the crucivorous *Pieris* in this community.

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INTERACTIONS BETWEEN BLOW FLIES (CALLIPHORIDAE) AND
ENTOMOPHTHORA BULLATA (PHYCOMYCETES:
ENTOMOPHTHORALES)

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Abstract.—Studies of interactions between blow flies and *Entomophthora bullata* showed that: (1) the time between exposure to conidia and death of the fly ranged from 5 to 12 days with about 50% dying by day 6; (2) the fungus produced only conidia in 79% of the cadavers, resting spores in 18%, and a mixture of the two in 3% of them; (3) in flies $\frac{1}{2}$ to 3 days old at exposure only conidia were formed in >80% of the cadavers, while in flies 4 to 5 days old at exposure only resting spores were formed in about 50% of the cadavers; (4) the death rates of flies were not influenced by their ages at exposure; and (5) the time required for the disease to kill flies was not related to the types of spores formed on or in their cadavers. Host species included *Phormia regina*, *Phaenicia sericata*, and *Protophormia terraenovae*.

Introduction

On August 10, 1973, I found two fresh cadavers of black blow flies, *Phormia regina*, that had apparently succumbed to a mycosis in a cage of miscellaneous muscoids taken alive two days earlier from a trap set in a wooded area near Ithaca, New York. I tied both cadavers to the wet wick of a water bottle which rested on a layer of moist sand within a glass battery jar. The jar, covered with clear polyethylene wrap to maintain a relative humidity close to saturation, was held overnight in a dark and cold room (14–16°C). By the following morning a reddish tan mycelial mat had grown over one cadaver; only the dorsum of its thorax remained uncovered. A thick layer of conidia discharged from this cadaver covered the aluminum foil collar of the water bottle and portions of the wick as well. The body surface of the second cadaver exhibited no growths and this specimen was removed from the wick for further study. A sample of the conidial shower produced by the first cadaver was also removed from the wick for microscopical examination.

The body cavity of the second cadaver was filled with spherical and hyaline bullate resting spores that ranged from 38 to 58 μm in diameter. The discharged conidia from the first cadaver were hyaline and elliptical with an evenly rounded apex and a papillate base. These conidia ranged in size from 25–37 \times 11–17 μm . In conformation and size these resting spores and con-

idia compare very favorably with those described by MacLeod et al. (1973) for *Entomophthora bullata*. I therefore concluded that the fungus found in these *P. regina* was the same species.

The present study was done: (1) to develop baseline data on the *in vivo* culture of *E. bullata* and its effects on blow flies, and (2) to determine if an association exists between the age of flies at exposure to conidia and the time of their death due to *E. bullata* infections and the types of spores produced in their cadavers.

Materials and Methods

The *P. regina* cadaver that produced the conidial shower, noted in the first section of this paper, served as the source of inoculum for the infectivity tests. Thirty young, laboratory-reared *P. regina* adults were added to the battery jar containing the water bottle with this cadaver tied to its wick. As noted previously, the collar of the water bottle and portions of the wick were covered with a thick layer of conidia. The jar containing this contaminated bottle and the healthy flies was returned to the dark and cold room. On the following morning the jar was placed on a laboratory bench at room temperatures (21–27°C). Here the flies received some artificial light from overhead fluorescent lamps during each day for the duration of the experiment. A small dish of dry sugar-milk was added to the jar as a source of nourishment for the flies. Several small holes were punched in the polyethylene cover for ventilation. The flies were observed at daily intervals and dead ones were removed from the jar and examined for signs of *E. bullata* infections. The data pertaining to this specific test are presented in Table 1 (see Test 1). The same procedures were used in all of the subsequent infectivity tests. All of the *P. regina*, *Phaenicia sericata*, and *Protophormia terraenovae* tested came from clean laboratory cultures.

The results given in Tables 2 through 4 are pooled data from 49 separate tests. The number of flies used in any single test was variable and depended upon the number of flies available at the time. While records on the ages of flies were maintained, records on the sex ratios within the test groups were not. Flies that died without *E. bullata* infections and flies that lived for more than 12 days following exposure to *E. bullata* conidia have been omitted from the data presented in Tables 2 through 4. No flies living for more than 12 days died with *E. bullata* infections.

Results and Interpretations

The data in Table 1 show that 27 serial passages of *E. bullata* were achieved from August 1973 to March 1974. The failure to effect transmission for additional passages was linked to a bacterial septicemia found in most

Table 1. Fly-to-fly passages of *Entomophthora bullata* in adult blow flies during an eight-month period under laboratory conditions.

Test number	Date test started	Flies tested		No. cadavers as inoculum sources*	Percentage dying with <i>E. bullata</i> **
		Species	Age (days)		
1	13 Aug.	<i>P. regina</i>	1/2	1	79 (23/30)
2	20 Aug.	<i>P. regina</i>	4	2	40 (6/15)
3	28 Aug.	<i>P. regina</i>	1/2	2	22 (4/18)
4	5 Sep.	<i>P. regina</i>	5	1	11 (3/27)
5	13 Sep.	<i>P. regina</i>	1/2	1	44 (10/23)
6	20 Sep.	<i>P. regina</i>	1/2	1	31 (6/18)
7	26 Sep.	<i>P. sericata</i>	1/2	1	53 (8/15)
8	4 Oct.	<i>P. regina</i>	1/2	2	100 (17/17)
9	10 Oct.	<i>P. terraenovae</i>	1/2	2	100 (10/10)
10	17 Oct.	<i>P. sericata</i>	5	1	86 (12/14)
11	26 Oct.	<i>P. regina</i>	1/2	1	59 (17/29)
12	5 Nov.	<i>P. sericata</i>	1/2	1	74 (17/23)
13	12 Nov.	<i>P. regina</i>	1/2	3	92 (12/13)
14	21 Nov.	<i>P. sericata</i>	1/2	1	79 (11/14)
15	28 Nov.	<i>P. regina</i>	1/2	3	82 (28/34)
16	5 Dec.	<i>P. sericata</i>	1/2	1	58 (11/19)
17	13 Dec.	<i>P. regina</i>	1/2	3	83 (15/18)
18	26 Dec.	<i>P. sericata</i>	1/2	1	100 (10/10)
19	2 Jan.	<i>P. regina</i>	1	1	67 (8/12)
20	14 Jan.	<i>P. regina</i>	1	1	29 (2/7)
21	25 Jan.	<i>P. regina</i>	1	1	44 (4/9)
22	4 Feb.	<i>P. sericata</i>	1	1	54 (15/28)
23	12 Feb.	<i>P. regina</i>	1	5	40 (15/28)
24	21 Feb.	<i>P. regina</i>	3	3	67 (4/6)
25	6 Mar.	<i>P. sericata</i>	1	1	37 (7/19)
26	19 Mar.	<i>P. sericata</i>	1	1	6 (1/18)
27	27 Mar.	<i>P. regina</i>	1	1	50 (5/10)
28	4 Apr.	<i>P. sericata</i>	2	3	0 (0/22)

* Source for Test 1 was a field-collected *P. regina*; sources for subsequent tests were conidia-producing cadavers from the previous trial.

** By post-exposure day 12.

of the *E. bullata*-infected flies that died in Tests 23 through 27 (see Table 1) and this severely depressed the development of the fungus. Hence the numbers of infectious units to which the flies were exposed declined during these last five tests. The data in Table 1 show that the percentage of flies dying with *E. bullata* infections ranged from 6 to 100%, yet there is no obvious relationship between the numbers of cadavers used as inoculum sources and the percentages of flies that acquired the infection. In nearly all cases the cadavers were attached to the substrate by rhizoids. All three species of blow flies were susceptible to infection.

Table 2. Age of blow flies at time of exposure to *Entomophthora bullata* conidia and time of death due to infection.

Age in days		(No.)	Post-exposure days and percentage dying during each period								
			1-4	5	6	7	8	9	10	11	12
½ to 1	<i>P. regina</i>	(454)	0	14	45	15	14	6	4	0.5	1.5
	<i>P. sericata</i>	(225)	0	19	40	28	7	4	1.5	0.5	0
	Both spp.	(679)	0	16	43	19	11	5	4	0.5	1.5
2	<i>P. regina</i>	0	0	0	0	0	0	0	0	0	0
	<i>P. sericata</i>	(16)	0	0	0	56	0	13	25	0	6
	Both spp.	(16)	0	0	0	56	0	13	25	0	6
3	<i>P. regina</i>	(46)	0	0	23	43	24	4	2	2	2
	<i>P. sericata</i>	(14)	0	57	43	0	0	0	0	0	0
	Both spp.	(60)	0	13	27	33	18	3	2	2	2
4	<i>P. regina</i>	(18)	0	6	11	33	28	0	11	11	0
	<i>P. sericata</i>	(34)	0	12	34	29	17	3	6	0	0
	Both spp.	(52)	0	10	25	31	21	2	8	3	0
5	<i>P. regina</i>	(18)	0	0	83	17	0	0	0	0	0
	<i>P. sericata</i>	(14)	0	0	86	0	0	0	7	7	0
	Both spp.	(32)	0	0	84	8	0	0	4	4	0
All ages in both species		(839)	0	14	42	21	12	5	4	1	1

Flies died of *E. bullata* infections as early as day 5 and as late as day 12 following exposure to conidia with about 50% dying by day 6 and 75% by day 7 (see Table 2). The data presented also suggest that susceptibility to infection among flies ½ to 5 days old is about the same in all of these age classes, and in both species tested. The data on age classes presented in this table, however, do not suggest that age of the fly at exposure alters the time required for the disease to kill the fly, i.e. older flies die at about the same rate as younger ones.

The data in Table 3 show that the fungus produced conidia in 79% of the cadavers, resting spores in 18%, and a mixture of conidia and resting spores in 3% of them. In this last group very light conidial showers were produced from scanty mycelial mats that grew on the surfaces of abdomens that harbored some resting spores internally. The data in Table 3 suggest that age of the fly at time of exposure does influence the types of spores produced by the fungus in the cadavers; in more than 80% of the flies ½ to 3 days old at exposure only conidia were formed, while in about 50% of the flies 4 to 5 days old only resting spores were formed. This observation supports the suggestion of Wilding and Lauckner (1974) that resting spore formation occurs more frequently in older wheat bulb flies, *Leptophlemyia coarctata*, infected with *E. muscae*.

Table 3. Age of blow flies at time of exposure to *Entomophthora bullata* conidia and types of spores produced in their cadavers.

Age in days		(No.)	Spore types with percentages of each		
			Conidia	Resting spores	Conidia + resting spores
½ to 1	<i>P. regina</i>	(454)	81	15	4
	<i>P. sericata</i>	(225)	88	9	3
	Both spp.	(679)	84	13	3
2	<i>P. regina</i>	0	0	0	0
	<i>P. sericata</i>	(16)	94	6	0
	Both spp.	(16)	94	6	0
3	<i>P. regina</i>	(46)	86	7	7
	<i>P. sericata</i>	(14)	29	71	0
	Both spp.	(60)	73	22	5
4	<i>P. regina</i>	(18)	22	78	0
	<i>P. sericata</i>	(34)	68	32	0
	Both spp.	(52)	48	52	0
5	<i>P. regina</i>	(18)	56	44	0
	<i>P. sericata</i>	(14)	21	79	0
	Both spp.	(32)	41	59	0
All ages in both species		(839)	79	18	3

Table 4. Time of death of *Entomophthora bullata*-infected blow flies and types of spores produced in their cadavers.

Spore types	(No.)	Post-exposure days and percentages dying during each period								
		1-4	5	6	7	8	9	10	11	12
Conidia										
<i>P. regina</i>	(423)	0	13	37	22	15	6	4	1	2
<i>P. sericata</i>	(242)	0	16	44	30	6	1.5	1.5	0.5	0.5
Both spp.	(665)	0	14	40	25	12	5	3	0.5	0.5
Resting spores										
<i>P. regina</i>	(94)	0	2	63	6	16	9	2	0	2
<i>P. sericata</i>	(56)	0	23	41	16	9	0	7	4	0
Both spp.	(150)	0	10	55	10	13	6	5	0.5	0.5
Conidia + resting spores										
<i>P. regina</i>	(19)	0	0	42	58	0	0	0	0	0
<i>P. sericata</i>	(5)	0	0	100	0	0	0	0	0	0
Both spp.	(24)	0	0	54	46	0	0	0	0	0
All spore types in both species										
	(839)	0	14	42	21	12	5	4	1	1

Conidia or resting spores may be formed in flies dying from days 5 through 12 (see Table 4). This phenomenon was observed in both *P. regina* and *P. sericata*. The conidia-resting spores mixture, found only in flies ½ to 3 days old at exposure, occurred in specimens dying on days 6 and 7 only. The data in Table 4 do not suggest that the time required for the disease to kill the fly is related to the type of spores formed on or in their cadavers.

Discussion

Prior to the discovery of *E. bullata* in *P. regina* reported in the present study, this fungus has been found parasitizing several other species of blow flies and flesh flies in nature. Povah (1935) found it in blue bottle flies and MacLeod (1956) extended its host range to include *Sarcophaga aldrichi* and a *Calliphora* species. MacLeod et al. (1973) observed an outbreak of *E. bullata* infections in a field population of *S. aldrichi*, and suggested that the life cycle of the fungus involved alternating generations of conidia and resting spores. The results of the present study, however, clearly indicate that conidia or resting spores, and in some cases a mixture of the two, may be produced on or in the dead bodies of flies that acquired the infection by exposure to conidia only. The host range of *E. bullata* in nature probably includes many species of blow flies that share the same habitat, e.g. *P. regina*, *P. sericata*, and *P. terraenovae*.

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POST-INGESTIVE UTILIZATION OF PLANT BIOMASS AND
NITROGEN BY LEPIDOPTERA: LEGUME FEEDING BY
THE SOUTHERN ARMYWORM

J. Mark Scriber

Abstract.—Polyphagous southern armyworms, *Spodoptera eridania*, are extremely efficient at assimilating ingested biomass and nitrogen in foliage of forage legumes. Variable efficiencies of processing the digested food (E.C.D.) were observed, however, and these differences reflect metabolic costs which may be related to biochemical factors mediating varietal differences in host plant resistance to other kinds of insects. Armyworms are apparently able to compensate for low conversion efficiencies with increased consumption rates such that their relative growth rates (mg. gained/mg. tissue/day) are virtually independent of digestive efficiency. In fact, larval growth rates of southern armyworms on these 15 legume varieties were among the greatest observed in a comparison with 22 other species of Lepidoptera in 140 similar feeding experiments. It appears that the combination of high leaf water content (80–91%) and high nitrogen content (4.2–5.5% dry) of legume foliage are key factors permitting such growth. Allelochemicals such as coumarin or the various saponins known to be present in these legumes were ineffective “barriers” to larval feeding and growth of armyworms in no-choice situations.

Introduction

The relative post-ingestive roles of allelochemicals and plant nutritional quality (e.g. leaf water content and leaf nitrogen content) in determining larval growth efficiencies have been analyzed for 22 species of Lepidoptera larvae feeding upon a variety of normal foodplant species (Scriber, 1978a). Foodplants used in these experiments ranged from trees (with leaf-water and nitrogen contents of 50% and 1%, respectively) to various groups of forb species with leaf-water typically in the range of 80% to 90% and nitrogen content ranging from 1.5% to 6.0%. In addition to a range of nitrogen concentrations provided by mature forb leaves, the Apiaceae (= Umbelliferae) (Kingsbury, 1964; Hegnauer, 1971) and the Cruciferae (Kjaer, 1974; Slansky and Feeny, 1977; and Chew, 1975) were chosen because of the unique array of allelochemicals encountered in the various species. In the study to be reported here, a variety of species of the Leguminosae were selected because of their high nitrogen as well as high water content, and also for the assortment of insect resistant genotypes (cultivars) which were

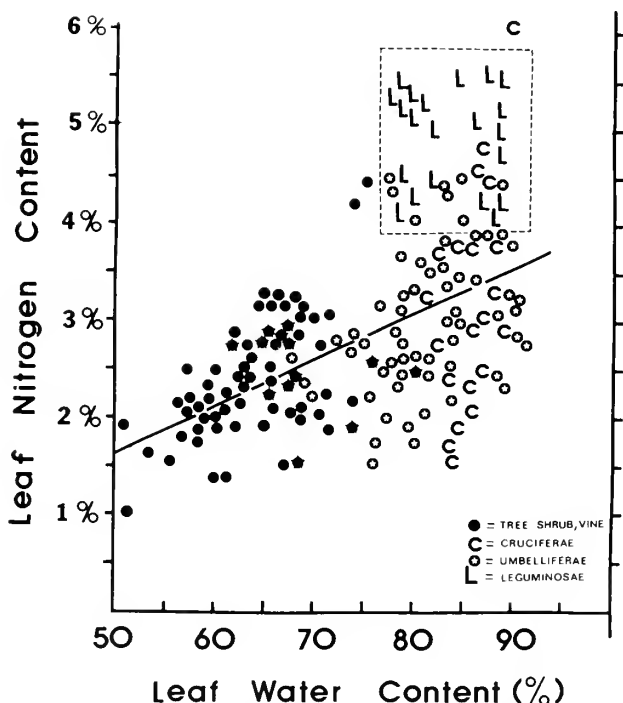


Fig. 1. The relationship of mean leaf nitrogen content and mean leaf water content of plants used for feeding experiments with various *Lepidoptera*. In this study the 15 legume varieties are indicated ("L") for comparison with 21 *Cruciferae* varieties ("C"), various *Umbelliferae* (starred), and additional vine, shrub, and tree species (solid circles) from experiments reported by Scriber (1978a). The six additional legumes are described by Scriber (1978b).

available for analyzing the relative growth suppressive effects upon the polyphagous southern armyworm, *Spodoptera eridania* (Cram.).

The possible importance of leaf water content in determining the larval growth of certain tree-feeding *Lepidoptera* has been described by Scriber (1977, 1979a). A comprehensive study of various swallowtail butterfly (*Papilionidae*) and silkmoth (*Bombycoidea*) species has revealed a striking correlation between larval growth and growth form of the foodplants (Scriber and Feeny, 1979). Leaf water content appears to provide a general indication of the larval performance to be expected from a variety of species of *Lepidoptera* of different sizes and different degrees of feeding specialization (Scriber 1978a). Just as the variance from the regression on leaf water of nitrogen content of mature leaves increased above 75% leaf water content (Fig. 1), so does the variance in larval performance (Scriber, 1978a; Scriber and Feeny, 1979). Larval performance (the consumption, assimilation, and

conversion of plant biomass and nitrogen for tissue growth) of forb feeders is generally much better than tree leaf feeders, and larval growth rate (mg. gain/mg. dry tissue/day) of herb feeders is generally $2\times$ – $6\times$ that of tree feeders.

Although the patterns of biomass and nitrogen accumulation rates between tree- and forb-feeding larvae are rather striking (Scriber and Feeny, 1979), we do not know the relative contributions of low nitrogen, high fiber, high tannin or other factors which could be involved in suppressing larval growth rates upon mature tree leaves. Furthermore, seasonal variations in nutritional quality of tree leaves are certainly of prime concern to lepidopteran herbivores (see Feeny, 1970, 1976; Rhoades and Cates, 1976). Seasonal variation in nutritional quality of forbs is also a very important factor determining larval growth rates and also may be more important than qualitative plant allelochemicals in determining utilization efficiencies of the Umbelliferae by 'adapted' herbivores (Finke, 1977). Of course, nutritional quality will be much less important when qualitative (behaviorally deterrent) allelochemicals are encountered by "unadapted" herbivores (see Erickson and Feeny, 1974; Feeny, 1975; Blau et al., 1978).

Any limiting effects of leaf water would presumably be less obvious for larvae feeding on plant tissues with 75–90% water content (e.g., forbs). It may thus be more likely that leaf nitrogen or allelochemical content would play more significant roles in determining the post-ingestive utilization of forb tissues for larval growth. Slansky and Feeny (1977) analyzed utilization of various Cruciferae species by larvae of an 'adapted specialist,' *Pieris rapae* L. They suggest that nitrogen is indeed in limiting supply (81–90% leaf water content) and that larvae increase their feeding rates on plants which are low in nitrogen content in order to maximize the nitrogen accumulation rate ($N.A.R. = \text{Nitrogen Consumption Rate} \times \text{Nitrogen Utilization Efficiency}$). The consumption rate of nitrogen was apparently increased up to a point beyond which declining nitrogen utilization efficiency (N.U.E.) offset the gain. It was suggested that consumption rate on any particular crucifer species would be adjusted to the lowest value at which maximal N.A.R. could occur. Although at least 19 different glucosinolates were reported from leaves of these foodplants, there was no detectable correlation between larval growth rate and these patterns of allelochemicals. Perhaps the importance of nitrogen in this study of Cruciferae-adapted larvae may have obscured any subtle allelochemical effects.

The independent roles and synergistic effects of leaf-water content, leaf nitrogen and allelochemicals on larval growth are very difficult to assess. The use of allelochemicals in artificial diet studies (Reese and Beck 1976a, b, c) or plants which are polymorphic for allelochemicals (Scriber, 1978b) allow some control of variables. Regulation of diet water content in artificial diets (Reese, 1977; Reese and Beck, 1978) or in natural foodplant leaves (Scriber,

1977) permits additional assessment of the relative importance of water in relation to other aspects of the diet. Fertilization to increase plant nitrogen content generally results in increased leaf water content as well (see Slansky and Feeny, 1977), and may not permit one to distinguish between effects to be attributed to these two variables.

It was the intent of the present study to attempt an assessment of the effects on larval growth of various plant characteristics of the Leguminosae family. In this study, the leaf-water content was relatively high (80–91%) and the plant nitrogen content was also generally high (4.2–5.5%). It was thus hoped that any differences in larval performance on 15 forage cultivars would not primarily be reflections of leaf-water and nitrogen limitations, but instead might reflect the more subtle post-ingestive effects of various biochemical factors implicated in host-plant resistance.

Methods and Materials

Fifteen Legume species selected and bred for agronomic qualities and insect resistance were fed to larvae of the southern armyworm (*S. eridania*). Growth performances on alfalfa varieties (Apollo, Arc, Culver, Kanza, MSA-CW3-AN3, Ranger, Riley, Team, Vernal, and Weevilcheck) were compared and contrasted with bird's foot trefoil, *Lotus corniculatus*; red clovers (Arlington and Lakeland); white clover; and yellow blossom sweet clover in these bioassays. Glasshouse-grown seedlings about 12 inches in height were used.

Consumption rates, assimilation efficiencies, conversion efficiencies and relative accumulation rates of biomass and nitrogen were determined for larvae via gravimetric methods (see Waldbauer, 1968; and Scriber 1977, 1978b for methods). These values were compared to those for other Lepidoptera as reported in Scriber (1978a), and in the figures presented here, the regression lines are calculated based on the means for the previous 140 experiments and do not include the 15 legume experiments.

Environmental conditions were virtually identical for all experiments reported (16:8 hr. photo: scotophase with a corresponding temperature regime of 23:19 °C). Included in these comparisons are experiments of Slansky and Feeny (1977) and Finke (1977) as well as those of Scriber (1975, 1978a, 1978b, 1979b) and Scriber and Feeny (1979).

Results and Discussion

As larval performance is surveyed over a range of foodplants from trees (with leaf-water contents of 50–75%) to forbs (with leaf-water contents of 75–95%), it becomes obvious that herb leaves are generally consumed more rapidly and converted to larval biomass more efficiently than tree leaves (Scriber 1978a). Legumes analyzed in this study support these general pat-

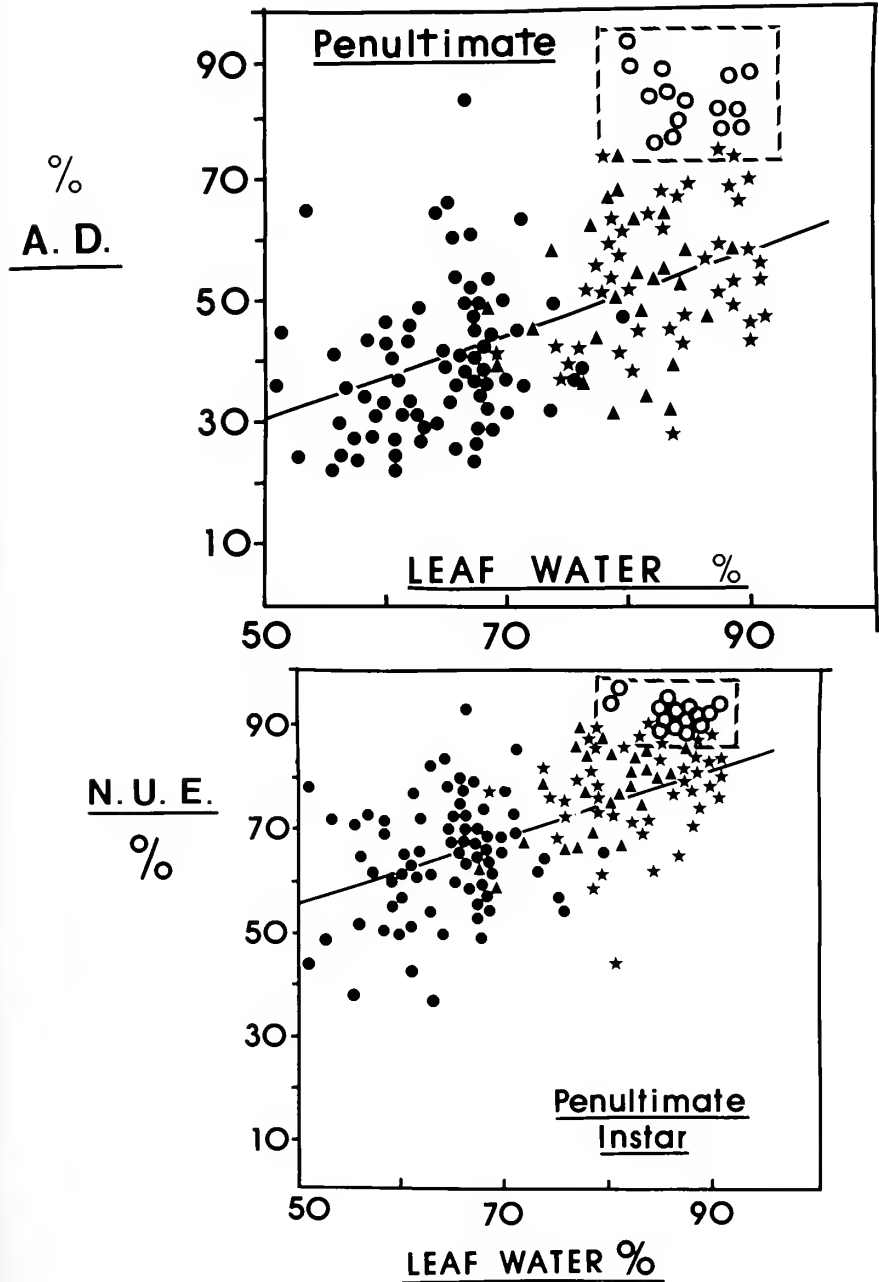


Fig. 2. Approximate digestibilities (Fig. 2a) and nitrogen utilization efficiencies (2b) of 22 species of lepidoptera in their penultimate instar as a function of leaf water content of their foodplants ($n = 155$). Trees, shrubs and vines are indicated by a solid circle, forbs are indicated by stars and triangles, and legumes by open circles (cf. Scriber, 1978a).

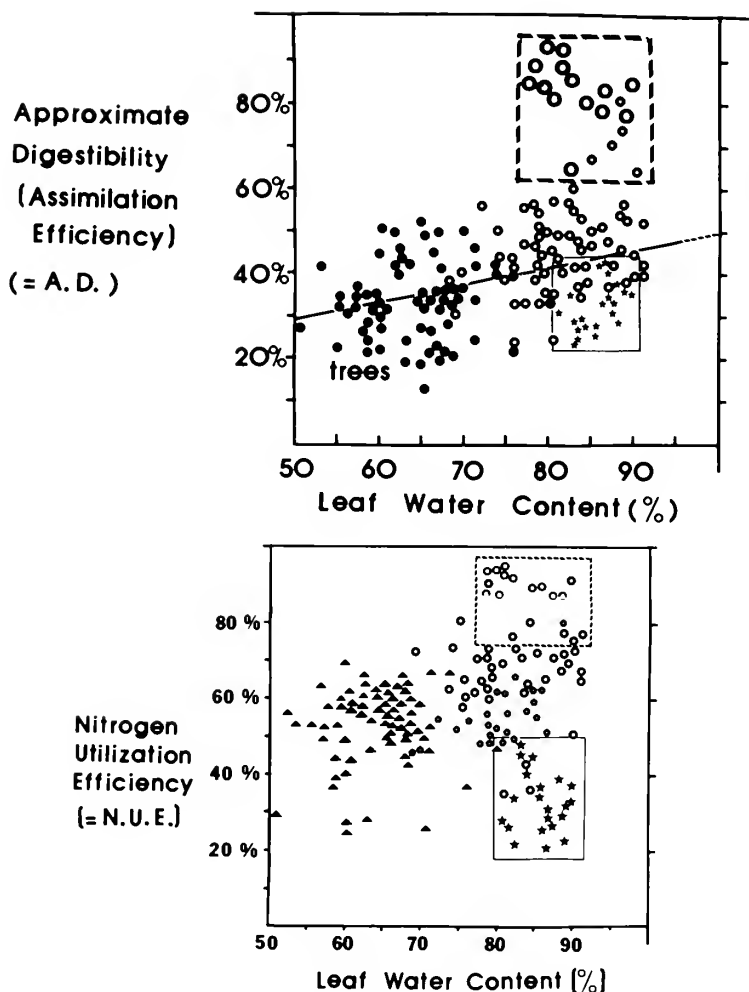


Fig. 3. Approximate digestibilities (Fig. 3a) and nitrogen utilization efficiencies (Fig. 3b) of final instar Lepidoptera as a function of leaf water of their foodplants ($n = 170$ experiments). The legume experiments are indicated by open circles and the Cruciferae by stars (cf. Scriber, 1978a). Solid symbols represent tree species.

terns, but more striking was the efficiency with which larvae were able to assimilate legume biomass and nitrogen in relation to penultimate instar lepidoptera in 140 other feeding experiments. The biomass assimilation efficiency or approximate digestibility (A.D.) of legumes by penultimate instar larvae ranges from 76 to 94% (Fig. 2a), and nitrogen utilization efficiencies (N.U.E.'s) from 89 to 96% (Fig. 2b). This pattern was also observed for

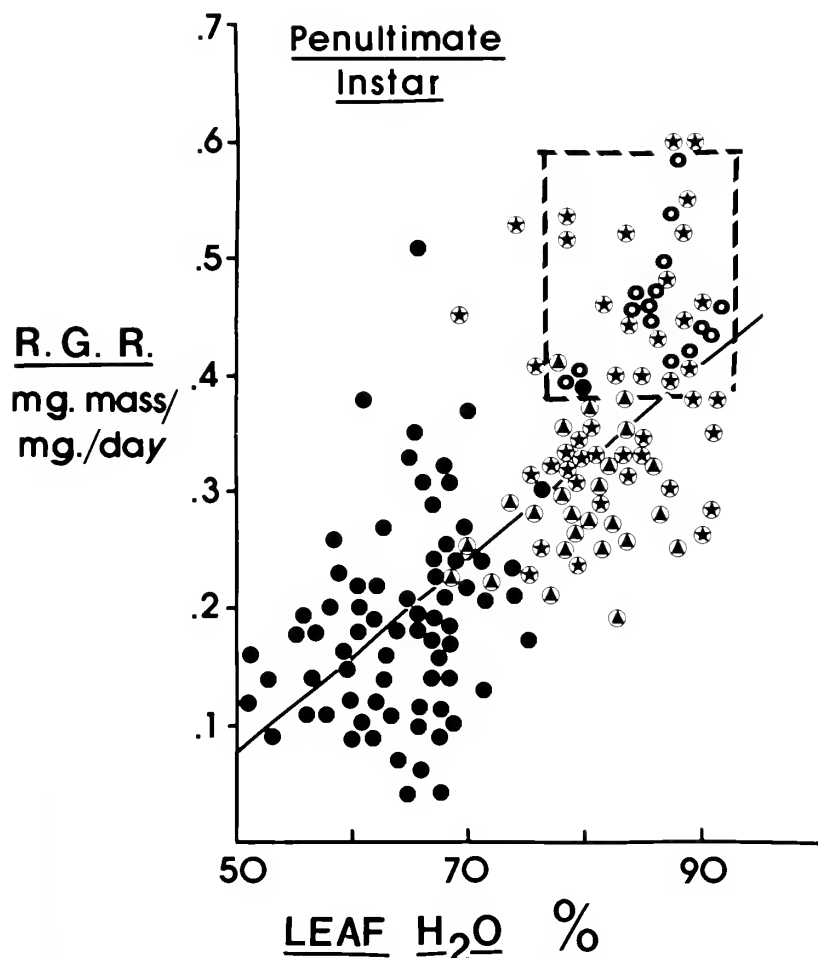


Fig. 4. The relative growth rates of penultimate instar Lepidoptera larvae as a function of the average leaf water content of the foodplant reared upon. The regression line was calculated previous to the inclusion of the 15 legume experiments (open circles).

legume-fed larvae in the final instar. The A.D.'s ranged from 64–92% and N.U.E.'s from 76–95% (Figs. 3a, 3b).

When performance data of final instar *Pieris rapae* on various Cruciferae (Slansky and Feeny, 1977) were compared to those of Umbellifer- and Legume-feeding lepidoptera, it appears that the Cruciferae may uniformly restrict the assimilation of biomass (A.D.) and nitrogen (N.U.E.) by *P. rapae* larvae (Fig. 3a and 3b respectively). While low efficiency of assimilating nitrogen and biomass could be related to nutritional qualities of the Crucif-

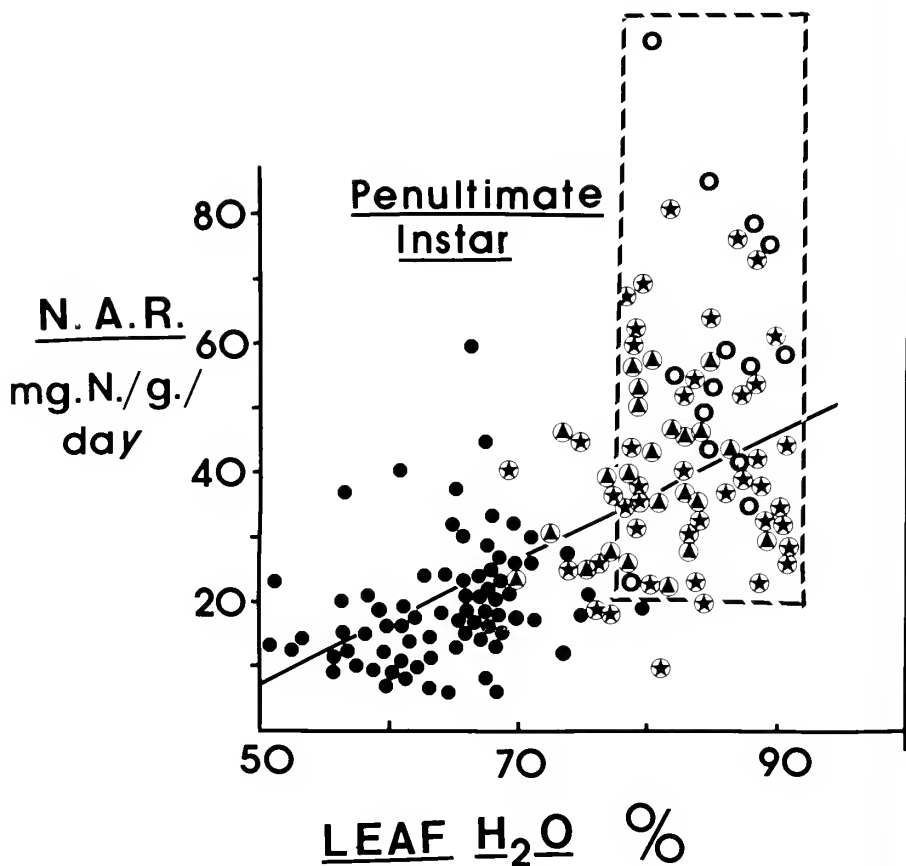


Fig. 5. The nitrogen accumulation rate (N.A.R.) of penultimate instar larvae as a function of leaf water content. Symbols represent the same plant types as in figure 2 and figure 4.

erae, perhaps glucosinolates should also be considered. These allelochemicals may thus have suppressive effects even upon Cruciferae-adapted specialists. While growth of *P. rapae* is not affected even by artificially high concentrations of allylglucosinolate (Blau et al., 1978), it appears that the larvae are able to compensate for low efficiency of assimilating crucifer leaf tissues by increased consumption rates (Slansky and Feeny, 1977; cf. Scriber, 1978a).

Umbellifer-feeding specialists (*Papilio polyxenes* and *P. zelicaon*) studied by Scriber and Feeny (1978) and Finke (1977) exhibited intermediate efficiencies in relation to *P. rapae* on Cruciferae and *S. eridania* on Leguminosae (Fig. 3a and 3b). Specialized forb feeders such as these species of

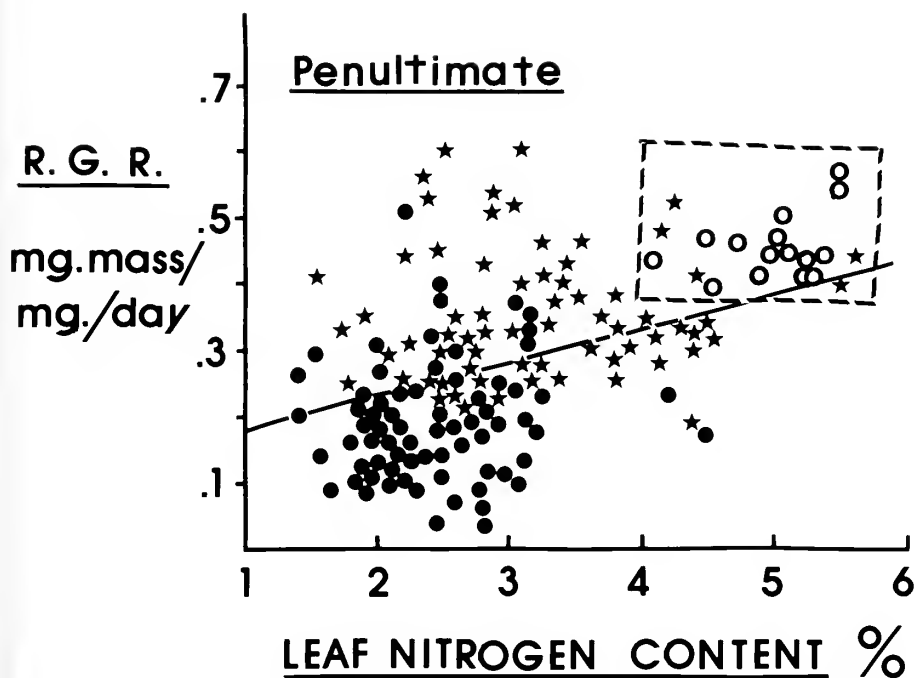


Fig. 6. Relative growth rate of penultimate instar larvae of 22 species of Lepidoptera as a function of leaf nitrogen content of their foodplants. Tree, shrub and vine plants are indicated by solid circles, forbs by stars, and legumes by open circles (See also Scriber, 1978a).

Umbellifer-feeding Lepidoptera grew at rates $2\times$ – $3\times$ those of the 18 species of tree, shrub and vine feeders (Fig. 4). Larval growth rates (R.G.R., Fig. 4) and nitrogen accumulation rates (N.A.R., Fig. 5) for the polyphagous *S. eridania* were also $2\times$ – $3\times$ greater than tree feeders as a group, suggesting that plant quality rather than degree of feeding specialization may be the more important influence.

Compared to the 22 species of Lepidoptera (Scriber, 1978a), larval growth rate is very fast for these armyworms on legumes. High nitrogen content (Fig. 6) as well as high water content (Fig. 4) is certainly a key contributing factor. While efficiencies of assimilating biomass and nitrogen are high for larvae on all of these forage legumes (Fig. 2 and 3), the efficiency of conversion of digested (assimilated) biomass (E.C.D.) was extremely variable. The low efficiencies of biomass conversion on Team (18.9%), Arc (24.1%) and Culver (29.8%) alfalfa varieties reflect greater metabolic costs for larvae than observed for other varieties (e.g. larvae fed Vernal and Apollo alfalfa had E.C.D.'s = 76.6% and 68.3% respectively, with 71.3% on yellow blossom sweet clover).

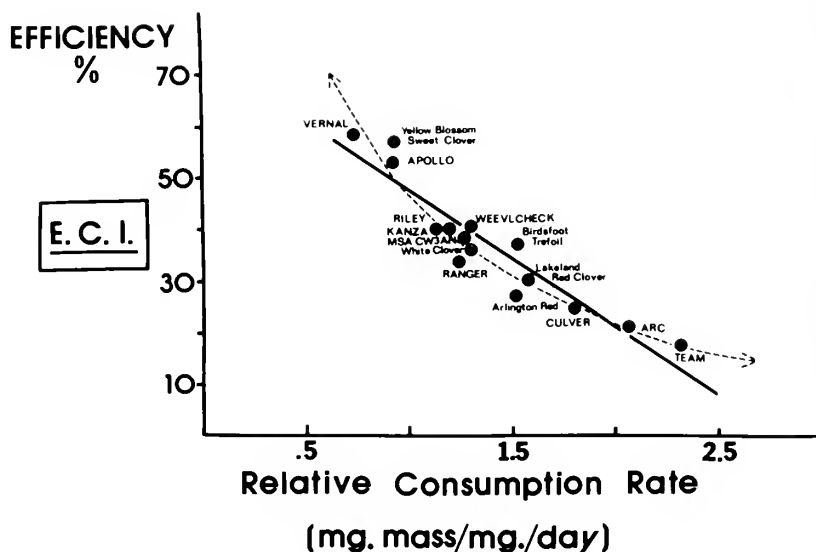


Fig. 7. The gross efficiency of growth ($E.C.I. = A.D. \times E.C.D.$) as a function of the relative consumption rate (R.C.R.) of plant biomass. Each symbol represents the experimental mean values obtained for penultimate instar *S. eridania* larvae on a particular legume variety. ($r = .937$; $n = 15$ for linear regression $Y = 74.2 - 26.6X$).

Why are certain genotypes more costly to process (in terms of assimilated energy and biomass) than others? Team, Arc and Culver alfalfa have been bred specifically for insect resistance to alfalfa weevil, aphids and meadow spittlebugs (Wilson and Davis, 1960; Barnes et al., 1970 and 1977; Sorensen et al., 1972), while Vernal and Apollo have been bred primarily for agronomic qualities and yield potential in Wisconsin (Rohweder et al., 1978). Concentrations of saponins, coumarin, cyanogenic glycosides and nitrates were not determined in this study. However, allelochemic variations between varieties can influence resistance to many insects (Horber, 1972; 1974; Manglitz et al., 1976; Pederson et al., 1976), and might be responsible for some of the variation metabolic costs experienced by armyworm larvae in the present study. Induction of the mixed function oxidase detoxication activity in *S. eridania* can be very rapid (Brattsten et al., 1977); however, it is premature to suggest that possession or operation of these enzyme systems is directly related to differential metabolic costs as measured here.

Nonetheless, polyphagous southern armyworm, *S. eridania*, is apparently able to compensate for the low efficiencies of conversion (i.e., high metabolic costs) on certain legume varieties by increased rates of food consumption (Fig. 7). This allows rapid growth in spite of the need to process a variety of potential allelochemicals in legume tissues. This 'power and efficiency'

trade-off (Odum and Pinkerton, 1955; Fig. 7) has not been observed for tree-feeding Lepidoptera (Scriber, 1978a). It has been suggested that in these cases low leaf water content may be a fundamental efficiency limiting factor and that increased consumption rates would perhaps only aggravate the problem (Scriber, 1977).

Conclusions

While some insects are effectively repelled, deterred or suppressed by different biochemicals in the 15 legumes used in this study, the southern armyworm is able to feed and grow successfully. Significant differences in metabolic costs of processing and converting plant biomass were reflected by E.C.D.'s (efficiency of conversion of digested food), which ranged from less than 20% to more than 75% on certain varieties. Larvae were, however, able to "compensate" by increasing their rate of consumption where efficiencies were low. It is suggested that this compensatory mechanism of maintaining larval growth rates near their maximum would be successful primarily where leaf water is not a limiting factor.

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OBSERVATIONS ON AGGREGATION AND OVERWINTERING IN
THE COCCINELLID BEETLE
COLEOMEGILLA MACULATA (DeGeer)

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Abstract.—In the overwintering site studied, *Coleomegilla maculata* began aggregating in late September to mid-October. The aggregation procedure appeared to be governed by photoperiod rather than temperature.

The major aggregation site studied included three major physical components: large prominent willow trees (*Salix nigra*); a small pond; and a south-facing slope. Migration to this site appeared to occur via a low level flight of positive anemotactic and hygrostatic nature, with the possibility of a hypostatic component. No chemotaxis was demonstrated, although the possibility was not ruled out.

Once at the aggregation site, beetles remained for some time on the leaves of wild raspberry (*Rubus occidentalis*) and sensitive fern (*Onoclea sensibilis*), especially the dead dry leaves of the latter. It is likely that this resting period on dry leaves assists in the loss of excess water.

Mortality of the beetles in the aggregation was 3% to 9% in the winter of 1973-74. Temperatures within the aggregation were generally higher than ambient temperatures, and the aggregation had a modifying effect on sudden temperature changes which might otherwise exceed the insect's ability to supercool.

Introduction

The massing of Coccinellid beetles for overwintering has been observed in many parts of the world. Aggregations are known to occur only in beetle species with abundant individuals which are closely associated with ephemeral prey or other food supplies which undergo seasonal fluctuation. Such is the case in *Coleomegilla maculata* (DeGeer) which, despite being markedly phytophagous in comparison to closely related coccinellids, aggregates to overwinter. Once the aggregation has been formed, the beetles exhibit a long dormancy period, often existing in below freezing temperatures. Overwintering *C. maculata* enter a state of ateleodiapause (after Mansingh 1971), as the beetles, upon disturbance, are capable of immediate but somewhat sluggish movement. In this state the overwintering adult generation survives for periods up to eight times the normal span of the summer generations.

The behavioral processes involved in migration toward an aggregation site, site selection and the formation of the aggregation vary widely in different species. According to Hagen (1962), *C. maculata* and *Hippodamia convergens* are the only two coccinellid species which do not exhibit simple hypsotactic aggregation. In *C. maculata*, a number of physical factors interact to guide the beetle to its aggregation site, so-called climatotactic aggregation. These factors and their interaction are, in the case of *C. maculata*, poorly understood. This paper reports observations of aggregating *C. maculata* and attempts to illuminate some of the processes used in aggregation site selection and migration.

Location

An aggregation site of *C. maculata* was discovered in 1971 in the town of Pomfret, Chautauqua County, New York. This site has been used each year for at least five years by aggregating beetles and was studied intensively from May 1973 to October 1974, and monitored periodically until May 1976. Unless specifically stated, observations recorded herein refer to this aggregation.

The aggregation was located near a small farm pond encircled by a clump of willow trees (*Salix nigra*), on the south-facing slope of a high bank which had resulted from digging the pond. The bank was generally covered with leaf litter and undergrowth. The area was about 100 meters north of extensive cornfields, and separated from them by a major rail line.

Three other aggregations, two in Erie County, New York and one in Cayuga County, New York, were discovered during the course of the study and were monitored periodically. The Erie County sites were also at the base of large willow trees. The Cayuga County site was at the base of a large poplar (*Populus deltoides*) in the front yard of a farm home and approximately 100 meters west of a large cornfield, and 50 meters north of another cornfield.

Field Observations

In 1973, the first influx of beetles at the aggregation site occurred on October 1, and in 1974 on September 28. These dates were either identical or approximate to arrival dates at the three other sites. Since the 1974 date followed several days of unseasonably hot weather (20°C), we felt that photoperiod rather than temperature was the signal for aggregation. In 1975, however, beetles arrived at the Cayuga County site on October 15, and date of arrival at the main site could not be determined. A few beetles were found on December 1, at a site about ten meters from the major aggregation sites of previous years, so that the exact time of aggregation is unknown. We believe that photoperiod is an important factor in the instigation of

Table 1. Temperatures (°F) at the three sites of overwintering beetles in the aggregation in Town of Pomfret, Chautauqua County, New York, in the winter of 1973-74.

Month	Site 1		Site 2		Site 3*	
	Low	Mean	Low	Mean	Low	Mean
December	27	42	24	37	24	39
January	21	33	22	35	15	31
February	14	39	12	41	8	31
March	20	44	14	42	13	38

* No beetles were present at this site after December.

processes leading to migration and aggregation, although it may not be the prime causal factor.

After the arrival of the first beetles, the aggregation grew rapidly and appeared to be complete within seven days of the initial arrivals. During the initial influx, clusters of beetles were found in depressions in the ground or at the base of saplings around the pond. These sites proved to be transitional, with the beetles eventually joining the main aggregation. The beetles formed three distinct clusters within the aggregation area. The largest of these clusters (site 1) contained the most beetles and was located around the base of the largest willow tree. Site 2 was established in a large depression near the entrance to a woodchuck hole, approximately 5 meters from site 1. The third site (3), containing the smallest number of beetles, was situated on the bank equidistant from sites 1 and 2. During early December the beetles at site 3 migrated to join those at site 1. The final two clusters at sites 1 and 2 covered little more than 0.5 square meters each, both being approximately 3 meters from the pond and elevated 1 meter above the water level. The location of the biggest cluster of beetles (site 1) near the base of the bank and at the base of the largest tree afforded maximum protection from the cold prevailing northerly winds moving in off nearby Lake Erie. At no time during the study were beetles found on the north-facing slope of the bank.

Having migrated to the aggregation site, beetles alighted on the upper sides of the abundant undergrowth species, including wild raspberry (*Rubus occidentalis*). Soon after arrival the beetles congregated on the undersides of the leaves and particularly under or in dead, dry, rolled up leaves of the sensitive fern (*Onoclea sensibilis*). Beetles on the undersides of leaves were generally immobile, while those on the upper surfaces (presumably newer arrivals) were more active. This pattern of arrival and subsequent association with dead vegetation was apparent throughout the aggregation formation. The reason for this is unclear but may be connected with the need to lose excess water, the freezing of which is thought to be the cause of some mortality among overwintering beetles (Hodson, 1937).

While in this situation, the beetles show a definite thermokinesis. Warmer periods induced greater activity but the beetles remained at the same levels on the vegetation. The thermokinetic response is, however, clearly complexed with other tactic responses as drops in temperature served to accelerate or instigate movement to the ground. Once on the ground, the beetles huddled under the top layers of loose soil and dead and decaying vegetation, where they remained for the duration of the winter.

Mortality

Maximum-minimum thermometers were placed among the three original aggregating groups of beetles at sites 1, 2, and 3. The thermometer at site 3 was left in place after the migration of the beetles to site 1. Sudden drops in temperature, thereby not giving the beetles sufficient time to supercool, are known to be the major cause of death in overwintering beetles (Hodson, 1937). During the winter of 1973-74, the temperatures never dropped below the level to which *C. maculata* can supercool successfully. Temperatures taken during the winter months (Table 1) show two main points. First, the "low" temperatures at sites 1 and 2 were higher than those at the beetleless site 3. Second, and more important, the "low" temperatures at site 2 were usually lower than those at site 1. This indicates the importance of the greater number of beetles at site 1 helping to maintain a higher temperature within the aggregation.

Actual mortality was determined by taking groups of beetles from the aggregation, placing them in wire mesh containers which afforded little extra protection, and replacing them in their original aggregation. At the end of the winter, mortality figures of 3% for site 1 and 9% for site 2 were obtained. In addition to the greater number of beetles at site 1, most of the beetles at this site were shielded from northwesterly winds by the presence of the willow tree whereas those at site 2 were not. This, together with the lower number of beetles, may account for the higher level of mortality observed at the more exposed site 2.

Discussion

The mechanisms and responses involved in triggering aggregation and in the migration to the aggregation site are difficult to elucidate due to their complex interactions. The possibility of a chemical cue being utilized in the selection of the aggregation site cannot be dismissed. Weiss (1913) felt that odor was important as an attractant to the aggregation site. However, during olfactory tests carried out on *C. maculata* no chemotaxis was found, the only consistent positive response being towards moisture-laden air. Landis (1936) showed that there is a significant difference in the reassociation of the Malpighian tubules in climatotactic as opposed to hypsotactically ag-

gregating species. Hodson (1937) also indicated that *C. maculata* showed a marked preference for specific moisture situations, suggesting that these were significant in reducing the effect of cooling by the latent heat properties of water. *C. maculata* is known to be very susceptible to desiccation and the ability of the beetle to detect and move towards moisture-laden air has been shown to affect its distribution in its summer habitat (Crump and Benton, in prep.). Adult *C. maculata* are larger and heavier than other closely related Coccinellids, including *H. convergens* which also undergoes climatotactic aggregation. The larger size, in conjunction with the predilection for moist areas and its profoundly pollenaceous diet, causes the low level flights and low distribution of *C. maculata* in vegetation (Ewert and Chiang, 1966). Short, low-level migratory flights would explain why many aggregations are found at or near the edges of open fields. Migration to the aggregation site is determined by positive hygrotactic and anemotactic responses complexed with a hypsotactic component causing aggregation at the bases of prominent objects in an area of optimum moisture level.

Aggregation of *C. maculata* serves as a method of enhancing winter survival, there being two aspects to this enhancement. First, the large number of beetles present emphasizes the aposematic coloration of the beetle. Second, and more significant, large numbers of beetles provide a degree of heat conservation. These factors combined with the biochemical mechanisms involved in the ateleodiapause of *C. maculata* ensure a greater survival rate over the arduous winter months.

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ON THE IDENTITY OF TWO SPECIES OF RHYPAROCHROMINAE
FROM ARGENTINA (HEMIPTERA: LYGAEIDAE)¹

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Abstract.—Two species described by Berg from Argentina in 1883 and 1884 and placed by him in the otherwise Palearctic genus *Tropistethus* have been restudied. Both species, *T. dubius* and *T. australis*, are considered to be distinct species in the genus *Cryphula*. A lectotype is selected for *Cryphula dubia* (Berg); redescriptions from type specimens are given for both species; a discussion is given of their relationships to other species of *Cryphula*. *Syngenicus* Berg 1883, listed as a provisional new generic name for *T. dubius*, is placed as a junior synonym of *Cryphula*. The lectotype of *Cryphula dubia* is figured.

In 1883 Berg described a new species of lygaeid from Argentina under the name *Tropistethus dubius*. Berg obviously had considerable doubt as to the correct generic position of this species as he stated that it might well represent a new genus and, indeed, went so far as to reserve the name *Syngenicus* for it in the event that it should prove to represent an undescribed genus. In the following year Berg (1884) described another new species from Argentina as *Tropistethus australis*. To my knowledge neither of these species has been subsequently discussed and the names only appear in faunal lists and catalogues (see Slater 1964).

Tropistethus Fieber is a Palearctic genus (nine species) in the tribe Antillocorini. I have recently been interested in the systematics and phylogeny of the Antillocorini of the Neotropics and have had an opportunity to examine the Berg types. As might have been anticipated neither species is congeneric with the Palearctic species of *Tropistethus*. Both species belong in the genus *Cryphula* Stål, a member of the rhyparochromine tribe Lethaeini. Both *dubius* and *australis* are, however, distinct from any described species of *Cryphula*.

Syngenicus Berg 1883 (type species *Tropistethus dubius*) thus becomes a junior synonym of *Cryphula* Stål (1874) (type species *Cryphula parallelogramma* Stål) NEW SYNONYMY.

Cryphula dubia (Berg) new combination

1883. *Tropistethus dubius* Berg pp. 265-266.

Berg described *dubius* from two males from Chacabuco ("Provincia Bon-aerensis") collected by Felix Lynch. I have examined both specimens which

¹ This work was supported by a grant from the National Science Foundation.

have identical labels saying (1) "Typus" (2) "Chacab. F. Lynch." Berg did not select a holotype and thus it is necessary to designate a lectotype. This is particularly important in the present instance as the two specimens probably are not conspecific.

Berg apparently thought he was dealing with brachypterous specimens. One syntype, indeed, is coleopteroid with only a narrow membrane vestige present. The second specimen, however, is a macropter with most of the membrane broken off, as is the distal portion of the right corium. There seems little doubt that Berg drew his description from the coleopter as he mentions the dark corial macula and testaceous legs which this specimen has but which is lacking on the mutilated macropter. Further a third label apparently in Berg's handwriting saying "*Tropistethus dubius* Berg" is on the pin with the coleopter. Accordingly this specimen is selected as lectotype and an appropriate label attached.

Redescription of Male Lectotype of *Cryphula dubia* (Berg)
(Figure 1)

Head, pronotum, scutellum, a large ovoid macula in center of corium, and antennal segments three and four dark reddish brown. Tylus yellowish. A large macula at each humeral pronotal angle which narrows mesad, extreme apex of scutellum, entire hemelytra except as indicated above, first and second antennal segments, labium and legs bright yellow. Forefemora infuscated with brownish on proximal three-fourths. Pleural and ventral surfaces completely shining or subshining, reddish brown. Head and pronotum strongly polished and shining. Dorsal surface, especially hemelytra, clothed with elongate, erect and conspicuous yellow hairs.

Head broad, eyes almost in contact with anterolateral pronotal angles; tylus broad distally reaching distal two-thirds of first antennal segment; head length .52¹, width .70, interocular space .50. Pronotum subquadrate, distance across anterior portion nearly as broad as that across humeri, anterior lobe conspicuously convex, posterior lobe narrow, lateral margins slightly sinuate; posterior margin shallowly concave, pronotum length .64, width .94. Scutellum length .58, width .58. Clavus and corium completely fused, commissure meeting evenly down midline, membrane vestige a narrow strip along apical margin of hemelytron and not extending posterior to caudolateral corner; lateral margins of hemelytron explanate and moderately arcuate, hemelytron length 1.40. Metathoracic scent gland auricle rather elongate, subtruncate, irregularly curving posteriorly. Evaporative area with distal (=dorso-lateral) margin evenly truncate, lacking shining intrusion anteriorly. Forefemora strongly incrassate, armed below near distal end with three short sharp spines followed proximally by two or three

¹ All measurements are in millimeters.

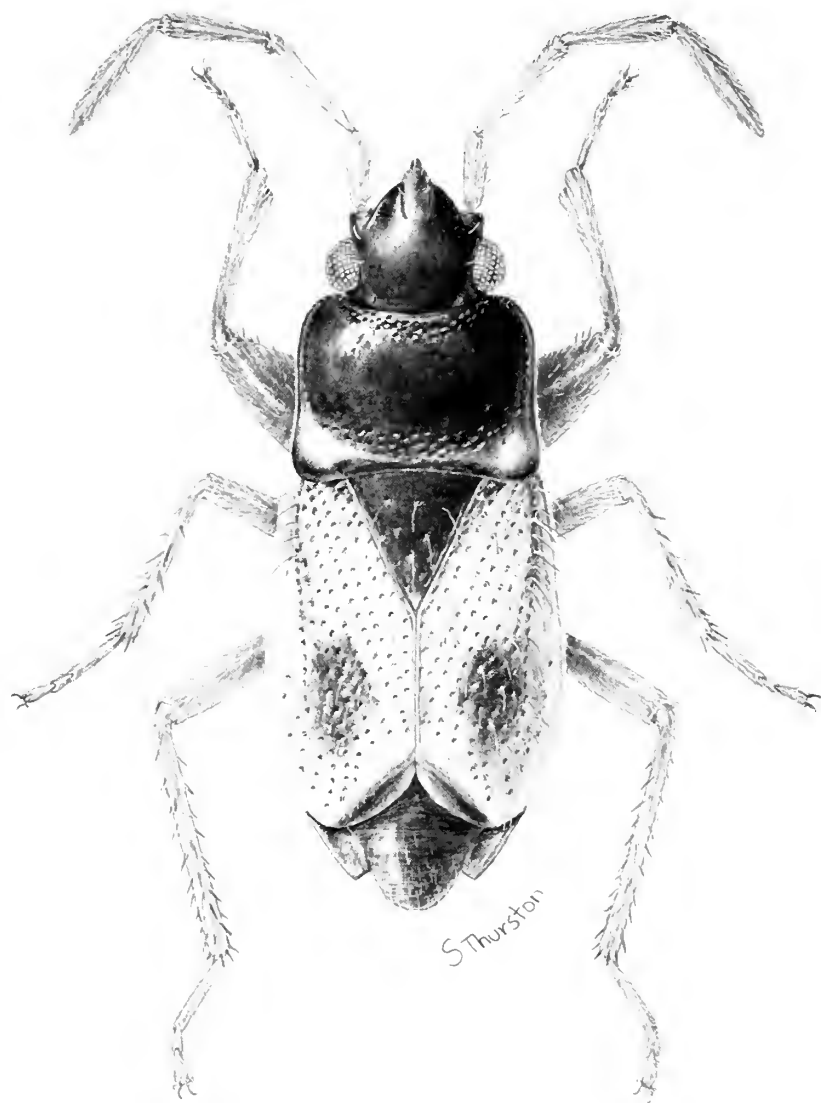


Fig. 1. *Cryphula dubia* (Berg) Lectotype. Dorsal view.

very elongate conspicuous spines. All tibiae with coarse spines present over surface. Antenna stout, typical of genus, antennal segment lengths I .28, II .48, III .46, IV .58. Labium probably attaining hind coxae, length labial segments I .40, II .32, III .36, IV .30.

The lectotype of *Cryphula dubia* has numerous elongate, erect hairs on dorsal surface. It will run to *Cryphula abortiva* Barber at couplet four in Scudder's (1962) key to the species of *Cryphula*. It is, however, not closely related to *abortiva*, differing in having pale testaceous hemelytra with a dark median macula, pale yellow humeral maculae, pale first and second antennal segments and a highly polished pronotum. *C. dubia* is rather similar in habitus to the recently described *Cryphula bennetti* Baranowski and Slater by virtue of the pale first and second antennal segments and legs, dark corial macula, pale humeral spots and dark scutellum. *C. bennetti*, however, lacks elongate hairs on the dorsal surface, has the rows of hemelytral punctures outlined as a series of dark stripes, has much larger humeral maculae, more evenly arcuate lateral pronotal margins and a white posterior metapleural lobe.

The other syntype of *dubius* is in poor condition. In addition to the broken membrane the antennae, fore tibiae and tarsi are all missing, and the specimen is greasy. It appears to be a species of *Cryphula* although in habitus it also resembles species of *Valtissius* Barber. The poor condition of the specimen makes it inadvisable to attempt to place it further taxonomically.

Cryphula australis (Berg) new combination

1884. *Tropisthetus* [sic] *australis* Berg, pp. 187–188.

Berg described *australis* from a single female from "Tandil" collected by "Dr. Holmberg." The holotype is a conventional looking *Cryphula* and runs in Scudder's (1962) key to *Cryphula apicata* (Distant) at couplet 6. Through the kindness of Mr. W. R. Dolling of the British Museum I have been able to examine Distant's lectotype of *apicata*, a male which was described from "S. Gerónimo, Guatemala." The types of *australis* and *apicata* are not conspecific. In *australis* the lateral pronotal margins are distinctly sinuate whereas in *apicata* they are evenly although narrowly arcuate. The membrane of *apicata* is dark brown with contrastingly pale veins, that of *australis* is white with a very large chocolate brown macula occupying most of the center of the surface. The posterior lobe of the metapleuron of *australis* is white and strongly contrasting with the anterior lobe, whereas in *apicata* the posterior metapleural lobe is reddish brown and concolorous with the anterior lobe. In *apicata* the metathoracic scent gland auricle is more elongate than it is in *australis* and slightly enlarged and subtruncate on the distal end, whereas it is subacute in *australis*. The adjacent evaporative area of *apicata* is invaded near its anterodorsad edge by a mesally

projecting "finger" of shining surface whereas in *australis* the dorsolateral margin of the evaporative area is straight throughout. *C. apicata* is extremely closely related to *C. nitens* Barber with which it agrees in all of the above characteristics. In fact, the specific status of *apicata* and *nitens* needs further study. Barber (1955) differentiated *nitens* from *apicata* by the former having the antennae "provided with several long semi-erect setae," by having "less conspicuous veins of the corium" and by differences in the color of the pronotum. I have examined specimens of *nitens* from Utah, California and Texas and cannot find differences in antennal hairs or degree of corial color differentiation between these specimens and the lectotype of *apicata*. *C. apicata* does have the pale coloration of the posterior pronotal lobe more prominently and extensively developed. I think the status of *nitens* questionable and in need of careful analysis.

Redescription of Female Holotype of *Cryphula australis*

Head, pronotum (except anterior margin, humeral angles and irregular extensions over posterior lobe on either side of midline), scutellum (except apex) and a very large ovoid distally irregular macula in center of hemelytral membrane reddish to chocolate brown. Remainder of dorsal surface white to light testaceous, hemelytral punctures darker brown forming irregular dark stripes. Nearly uniformly dark reddish brown below, shining, with dorsal portion of posterior propleural lobe and all of hind lobe of metapleuron a strongly contrasting white. Legs light yellow with anterior femora yellowish brown on proximal three-fourths. Dorsal surface nearly glabrous lacking elongate upstanding hairs.

Head slightly declivent, conspicuously convex between eyes, latter in contact with anterolateral angles of pronotum, head length .58, width .76, interocular space .50. Pronotum with lateral margins narrowly but conspicuously explanate and markedly sinuate, posterior margin shallowly concave before scutellum, pronotum length .68, width 1.24. Scutellum length .74, width .76. Claval commissure length .36. Lateral margins of corium explanate and evenly arcuate. Distance apex clavus-apex corium .54; distance apex corium-apex membrane .58. Metathoracic scent gland auricle finger-like tapering distally, evaporative area with dorsolateral margins evenly truncate, complete. Forefemora strongly incrassate, armed below near distal ends with two very sharp spines followed proximally by three conspicuous elongate hairs. Antennae missing. Labium extending well between and probably slightly beyond posterior margin of mesocoxae, perhaps reaching metacoxae, length labial segments I .38, II .40, III .36, IV .30; total length 3.36.

Redescription of Lectotype of *Cryphula apicata* Distant

Head, major part of pronotum and scutellum dark chocolate brown. Anterior marginal area of pronotum, elongate elliptical macula in area of humeri and three conspicuous spots along posterior margin of pronotum white to very pale testaceous. Hemelytra variegated, veins conspicuously white or pale yellow, intervening areas reddish brown mottled with testaceous and with a conspicuous small pale elliptical macula present near apical margin between radius and medius. Membrane brown with veins a strikingly contrasted translucent white. Antennae yellowish, distal third of segment three and all of segment four darker. Legs pale reddish brown becoming testaceous distally. Ventral and pleural surfaces including posterior lobe of metapleuron bright red brown but with pale yellow to white coloration present along dorsal portion of posterior lobe of propleuron. Dorsal surface nearly glabrous lacking conspicuous upstanding hairs.

Head slightly declivent, moderately convex between eyes, tylus broad reaching at least to distal fourth of first antennal segment, head length .50, width .72, interocular space .46. Pronotum subquadrate, lateral margins narrowly explanate evenly curving or gently arcuate from humeri to anterolateral angles, pronotum length .76, width 1.22. Scutellum length .76, width .72. Claval commissure length .38. Corium very slightly arcuate, nearly straight for greater portion of length. Distance apex clavus-apex corium .70, distance apex corium-apex membrane .44. Metathoracic scent gland auricle elongate slightly broadened and subtruncate at distal end, evaporative area with deep finger-like shining intrusion into dorsolateral margin near anterior end of metapleuron. Forefemoral armature and labial length obscured, latter apparently reaching at least well between mesocoxae. Antennal segment lengths I. 24, II .48, III .38, IV .46. Total length of body 3.32.

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INTRODUCED PARASITES OF *AGROMYZA FRONTELLA*
(RONDANI)¹ IN THE USA

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Abstract.—From 1974 to 1978, we released 14 species of European parasites (ca. 82,000 insects from 3 agromyzid host species on alfalfa) as part of a biological control effort against the alfalfa blotch leafminer, *Agromyza frontella* (Rondani), in the USA. A list of release locations, dates, and parasite numbers is presented. Techniques for rearing 4 of the species are briefly described. Two species, *Dacnusa dryas* (Nixon) (Hymenoptera: Braconidae) and *Chrysocharis punctifacies* Delucchi (Hymenoptera: Eulophidae), have been established in Delaware. Sufficiently large field populations of these species were present in 1978 so that insects were collected by sweeping and moved to other release locations.

The alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani), a pest of European origin first reported in the USA in Massachusetts in 1968 (Miller and Jensen, 1970), is now found throughout the northeastern states and adjacent Canadian provinces. The USDA began the introduction of parasites for biological control of this pest in 1974. The purpose of this paper is to document parasite releases and recoveries.

Sources of parasites released.—Foreign parasite material was provided by the USDA European Parasite Laboratory, Sèvres, France. The material was received at our laboratory quarantine facility as adults or as immatures in host puparia. Several parasite species were reared successfully in the laboratory, and releases were made from these cultures. By 1978, 2 species of parasites, *Dacnusa dryas* (Nixon) and *Chrysocharis punctifacies* Delucchi, became so abundant in local fields that they were collected by sweeping and moved to new release locations. The order, family, and determiner of all parasite and host species mentioned in this paper are listed in Table 1. Releases of 14 species of European parasites (ca. 82,000 insects from 3 agromyzid host species on alfalfa) against ABL were made from 1974 to 1978. The species, numbers, and locations are found in Table 2.

Techniques for rearing parasite species.—We attempted to rear nearly all of the 14 parasite species but were successful with only 4 of them. (Since the use of ABL as a host means that considerable space must be provided for potted alfalfa and relatively few ABL per plant are produced, we used alternate hosts whenever possible.)

¹ Diptera: Agromyzidae.

Table 1. Order, family, and determiner of species mentioned in this paper.

Species
HYMENOPTERA: BRACONIDAE
<i>Chorebus</i> poss. <i>misellus</i> (Marshall) ^a
<i>Dacnusa dryas</i> (Nixon) ^a
<i>Dacnusa maculipes</i> Thomson ^a
<i>Dacnusa</i> sp. ^a
<i>Dapsilarthra balteata</i> (Thomson) ^e
<i>Opius duresseui</i> Fischer ^a
<i>Opius maculipes</i> (Thomson) ^a
<i>Phanomeris braconius</i> (Haliday) ^a
HYMENOPTERA: EULOPHIDAE
<i>Chrysocharis naenia</i> (Walker) ^f
<i>Chrysocharis punctifacies</i> Delucchi ^f
<i>Diglyphus intermedius</i> (Girault) ^b
<i>Diglyphus isaea</i> (Walker) ^b
HYMENOPTERA: PTEROMALIDAE
<i>Halticoptera circulus</i> (Walker) ^f
<i>Miscogaster hortensis</i> Walker ^d
<i>Miscogaster maculata</i> Walker ^d
DIPTERA: AGROMYZIDAE
<i>Agromyza frontella</i> (Rondani) ^c
<i>Agromyza nana</i> Meigen ^c
<i>Agromyza parvicornis</i> Loew ^c
<i>Liriomyza congesta</i> (Becker) ^c
<i>Liriomyza trifoliarum</i> Spencer ^c

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Chrysocharis punctifacies, a solitary endoparasite of larvae, emerging from puparia, was successfully reared on ABL by placing adult parasites in cages containing alfalfa plants that had mining larvae in the leaflets. After the parasites oviposited, the plants were laid on their sides so mature parasitized hosts dropped from the leaflets into trays of moist vermiculite from which they eventually emerged. This is a slight modification of the tipped plant method for rearing ABL described by Hendrickson and Barth (1977). The parasite also oviposited readily on *Liriomyza trifoliarum*, reared on bean plants, but this leafminer invariably died after transforming to the pupal stage, and no parasites developed.

Dacnusa dryas, another solitary endoparasite of larvae, emerging from puparia, was successfully reared on ABL by using the same techniques

Table 2. Releases of European parasites against the alfalfa blotch leafminer in the USA. Original host species are indicated in footnotes.

State	County	Locality	Release year (19—)	No.
<i>Chorebus poss. misellus</i> ^{a,c}				
Delaware	New Castle	Newark	77	132
<i>Chrysocharis naenia</i> ^{b,c}				
Delaware	New Castle	Newark	77	28
New Jersey	Warren	Blairstown	78	5
			Total	33
<i>Chrysocharis punctifacies</i> ^a				
Delaware	New Castle	Newark	77	1,277
			78	217
New Jersey	Burlington	Rancocas	78	100
			78	35
New York	Cortland	Cortland	78	255
			78	16
			78	163
			78	338
Ohio	Ashtabula	Padanaram	78	29
Pennsylvania	Chester	Kemblesville	78	10
			78	10
			77	66
			78	791
			Total	3,307
<i>Dacnusa dryas</i> ^a				
Delaware	New Castle	Newark	77	620
			78	596
New Jersey	Burlington	Rancocas	77	12
			78	156
			78	126
New York	Cortland	Cortland	78	1,839
			78	30
			78	254
Ohio	Ashtabula	Padanaram	78	21
Pennsylvania	Chester	Kemblesville	78	50
			78	50
			77	55
			78	1,398
			Total	5,207
<i>Dacnusa maculipes</i> ^{b,c}				
Delaware	New Castle	Newark	77	352
Pennsylvania	Chester	Oxford	77	13
			Total	365

Table 2. Continued.

State	County	Locality	Release year (19—)	No.
<i>Dacnusa</i> sp. ^{a,b,c}				
Delaware	New Castle	Newark	76	10
			77	653
New Jersey	Burlington	Rancocas	77	97
Pennsylvania	Chester	Oxford	77	139
			Total	899
<i>Dapsilarthra balteata</i> ^{a,c}				
Delaware	New Castle	Newark	77	50
			78	3
Pennsylvania	Chester	Oxford	78	7
			Total	60
<i>Diglyphus isaea</i> ^{a,b,c}				
Delaware	New Castle	Newark	75	2,000
			76	16,295
Maryland	Cecil	Fair Hill	75	600
			76	2,000
Massachusetts	Hampshire	Hadley	75	600
New Hampshire	Grafton	Concord	75	600
New Jersey	Burlington	Rancocas	75	1,850
			76	13,800
	Warren	Blairstown	75	1,150
			76	2,500
New York	Orange	Windsor	75	400
Pennsylvania	Chester	Kemblesville	75	50
		New London	75	1,400
		Oxford	76	4,000
			75	950
	Schuylkill	Port Clinton	76	17,950
			75	400
			Total	66,545
<i>Halticoptera circulus</i> ^a				
Delaware	New Castle	Newark	78	5
<i>Miscogaster hortensis</i> ^a and <i>M. maculata</i> ^d				
Delaware	New Castle	Newark	75	34
			76	5
			77	355
			78	270
Ohio	Ashtabula	Padanaram	78	3
Pennsylvania	Chester	Oxford	77	70
			78	110
New Jersey	Burlington	Rancocas	78	8
	Warren	Blairstown	78	30

Table 2. Continued.

State	County	Locality	Release year (19—)	No.
New York	Cortland	Cortland	78	34
	Herkimer	Mohawk	78	3
	Tompkins	Dryden	78	71
	Total			993
<i>Opius dureseauli</i> ^{a,b}				
Delaware	New Castle	Newark	75	22
			77	127
			78	20
New Jersey	Warren	Blairstown	75	16
New York	Cortland	Cortland	78	51
	Herkimer	Mohawk	78	52
Ohio	Ashtabula	Padanaram	78	8
Pennsylvania	Chester	Oxford	78	13
Total				309
<i>Opius maculipes</i> ^b				
Delaware	New Castle	Newark	77	10
Pennsylvania	Chester	Oxford	78	45
Total				55
<i>Phanomeris braconius</i> ^{a,b}				
Delaware	New Castle	Newark	75	20
			76	320
			77	1,494
			78	741
New Jersey	Burlington	Rancocas	74	107
			77	148
			78	240
			74	8
	Warren	Blairstown	77	16
			78	190
			77	40
			74	31
Pennsylvania	Sussex	Vernon	74	31
	Chester	Oxford	76	20
			77	352
			78	357
	Landenberg	77	32	
Total				4,116

^a *Agromyza frontella*.^b *Agromyza nana*.^c *Liriomyza congesta*.^d Host relationships are uncertain due to a recent determination that 2 species of *Miscogaster* were involved, rather than an initial determination of 1 species.

described for *C. punctifacies*. When the parasite was exposed to *L. trifoliarum* on bean plants, only a few males were produced. However, both sexes emerged from *L. trifoliarum* collected at the laboratory field in 1978.

Diglyphus isaea, a larval ectoparasite of ABL, was initially reared on ABL infesting potted alfalfa plants. Once the parasites had oviposited on these larvae, the alfalfa stems were cut, and placed in emergence cages, and allowed to dry out. However, production of these parasites was limited by the relatively small numbers of host larvae available on potted alfalfa plants. Later, an easier and more productive method of rearing on *L. trifoliarum* on bean plants was devised (Hendrickson, 1975). In either case, the parasite had to be provided with 3rd-(mature) instar host larvae since it killed 1st- and 2nd-instar larvae by probing, usually without ovipositing.

Phanomeris braconius, a larval ectoparasite, was successfully reared on ABL by the methods described for *D. isaea*. Thus *L. trifoliarum* on bean plants was an acceptable host, but the technique was inefficient because the emerging parasites were small and too many host larvae developed into adult flies. Best results were obtained by rearing *P. braconius* on *Agromyza parvicornis*, a native pest of corn. After the parasites had oviposited on the host larvae, the corn culms (ca. 30-cm tall) were cut, placed in an emergence cage, and dried. Honey was provided as food for emerging parasites. The parasites obtained were slightly larger than those that developed on ABL.

Parasite establishments.—The following species were released at the laboratory alfalfa field in 1977 and recovered by rearing from ABL or by sweeping in 1978. The sampling and emergence techniques employed were described by Hendrickson and Barth (1979).

Dacnusa dryas was released at a rate of 750/ha. The parasite was first recovered from samples collected June 26, 1978 (2nd-cutting alfalfa) and was collected from subsequent samples through November. *Dacnusa dryas* was the most abundant parasite species during the period June 26–30, when it parasitized 14% of the ABL. On the basis of number of stems per m², number of mines per stem, and percentage of mines producing the parasite, we calculate that this peak emergence resulted in ca. 175,000 host larvae/ha later producing the parasite species. The rapid rate of increase in only a year is probably a result of a relatively high rate of parasite fecundity and the occurrence of 5 generations of ABL per year in the Delaware area.

Parasite adults were collected by sweeping (maximum recovery rate was 35/100 sweeps) and moved to other release locations. At first we aspirated the *D. dryas* adults from the sleeve cages where we placed the field material from the 100 sweeps. This procedure was time consuming, and separation of *D. dryas* from other insects was difficult. It was more efficient to put the unseparated field material from 1,000 sweeps (collected 200 at a time) into a large, styrofoam container cooled by a freeze pack wrapped in paper

towels. Then the material was taken to a release location. Mortality of material handled in this manner appeared to be slight.

Chrysocharis punctifacies was released at a rate of 190/ha in 1977. The parasite was first recovered on July 17, 1978 (3rd-cutting alfalfa) and was reared from samples collected through September. It was the most abundant parasite species during Sept. 18–22 when it parasitized 34% of the ABL. Adults were collected by sweeping (maximum recovery rate was 5/100 sweeps) and moved to release locations. We had the same difficulty separating adult *C. punctifacies* from field-collected material as we had in separating *D. dryas*, but in addition, several common native *Chrysocharis* species cannot be distinguished from *C. punctifacies* except under the microscope. Again this species was more efficiently disseminated locally by mass collections. However, we unexpectedly recovered a few *C. punctifacies* from field-collected *L. trifoliarum*. Possibly size of host explains our inability to rear the parasite in the laboratory (field-collected insects are larger than laboratory-reared specimens).

Parasites of uncertain establishment status.—A total of 86 *Miscogaster hortensis* and *M. maculata*, solitary endoparasites of larvae, emerging from puparia, was released in 1975–77 at the laboratory alfalfa field (release rate was 85/ha). (The European host relationships for *Miscogaster* spp. in Table 2 are uncertain because the initial determination was that only a single species was involved; later examination of a more extensive series of specimens indicated 2 species were involved.) No *Miscogaster* spp. emerged from samples collected in 1978, but several adult *M. hortensis* were collected by sweeping. Although the species has survived at least one winter, we believe recovery was too low to warrant a claim of establishment. The species may eventually become sufficiently abundant for unquestioned establishment and it may produce significant results.

Miscogaster spp. comprised 15% of the parasites emerging from European ABL puparia processed at the laboratory quarantine facility in 1976–77 and the genus was third in abundance after *C. punctifacies* and *D. dryas* (Hendrickson and Barth, 1979).

Diglyphus isaea, the most abundant parasite of ABL in Europe (J. J. Drea, Jr., pers. com.), was reared in the laboratory and released in large numbers in 1975–76. There were few recoveries in those years and none subsequently. Since *D. isaea* is very similar morphologically to the most abundant North American parasite attacking ABL, *D. intermedius*, we examined the hypothesis that these 2 species had hybridized. Crosses of *D. intermedius* ♀ with *D. isaea* ♂ produced fertile female progeny, but the reciprocal cross produced only males, which indicated that fertilization had not taken place. It therefore seems probable that some *D. isaea* genetic material has been added to the *D. intermedius* gene pool in the USA. How-

ever, *D. isaea* females appear to be reproductively isolated from *D. intermedius*, so their disappearance may have resulted from competitive displacement with *D. intermedius*, or from mating (without fertilization) with *D. intermedius* males, which were far more abundant in the field than *D. isaea* males.

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PHOTOPERIOD AND TEMPERATURE INFLUENCES ON
EGG NUMBER IN *BRACHYMERIA INTERMEDIA*
(HYMENOPTERA: CHALCIDIDAE), A PUPAL
PARASITOID OF *LYMANTRIA DISPAR*
(LEPIDOPTERA: LYMANTRIIDAE)¹

P. Barbosa and E. A. Frongillo, Jr.²

Abstract.—Oosorption in *Brachymeria intermedia* (Nees) is photoperiodically induced by a short photophase. Low temperatures enhance the effects of photoperiod. Oocyte resorption proceeded more quickly at lower temperatures. Preconditioning of immature stages within its host or of young adults has an effect on rate of oocyte resorption.

Insects exhibit a variety of reproductive mechanisms including viviparity, ovoviviparity, oviparity, etc. In many species, particularly in parasitoid species, the timing of oviposition is critical. Appropriate timing of oviposition and conservation of nutrients may be enhanced by oosorption. Oosorption is a process characterized by cessation of vitellogenesis and degeneration of the vitellogenic oocyte within the ovary. It has been associated with various life history phenomena as an energy conserving reproductive strategy. That is, resorption is an adaptive mechanism which occurs when oviposition would waste energy. Resorption of oocytes in diapausing females has been described in a number of species including an ichneumonid parasitoid. It is also found in insects avoiding adverse conditions, characterized by low temperature or short day photoperiods (Bell and Bohm 1975).

The reproductive system of *Brachymeria intermedia* (Nees), a European pupal parasitoid of the gypsy moth, is typically hymenopteran (D'Rozario 1942), containing two ovaries each of which is comprised of three polytrophic ovarioles (Dowden 1935, Engleman 1970). A mature ovariole will usually hold one chorionic and one or two other vitellogenic oocytes. Thus, *B. intermedia* is a synovigenic species with monootene ovarioles where ovulation is externally induced (Flanders 1950). Flanders (1950) suggested that hymenopteran parasitoids that have synovigenic females are more likely to

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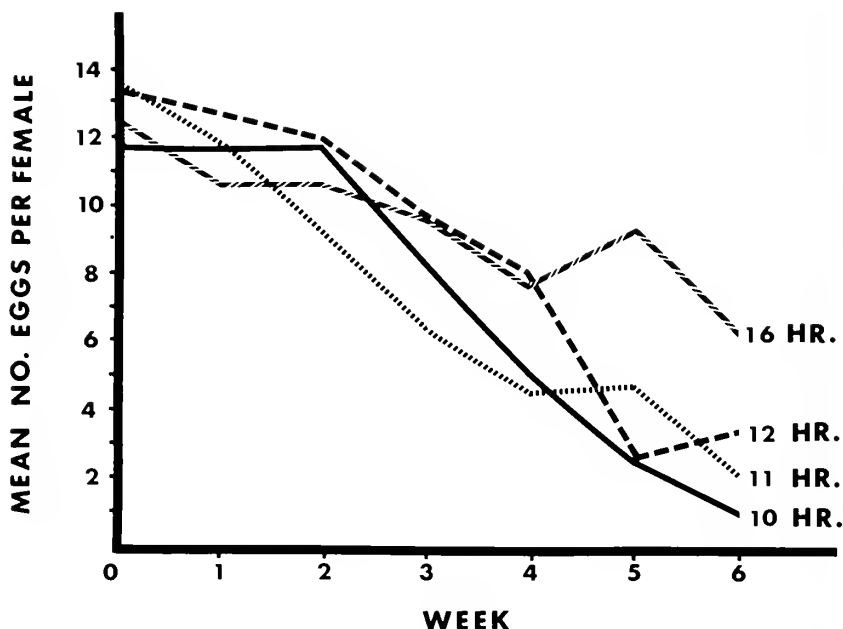


Fig. 1A. The influence of photoperiod on the average number of vitellogenic eggs in *B. intermedia*.*

be effective biological control agents, in part, because ovigenesis and oosorption are not totally host dependent. This study details the role of photoperiod and temperature on oosorption in *B. intermedia*.

Materials and Methods

B. intermedia were reared on wax moth pupae (*Galleria mellonella*), a standard laboratory host. Upon emergence, adults were maintained in 30 × 30 cm cages at 16 hr L:8 hr D, 50% R.H. and 21.1°C for two weeks before being used in experiments. In the laboratory, the achievement of reproductive maturity in females is variable but in general, females are mature after about 7 days. For each set of experimental conditions in each experiment groups of 80 females and 25 males were placed in a cage and provided with honey, distilled water and paper strips (resting sites).

Data on the initial state of the female reproductive system (week 0) was obtained by removing 10 females for dissection. On each of 6 successive weeks 10 females were dissected to determine the state of ovarian development. Each dissection involved the removal of the intact ovaries. Both the total number of opaque (vitellogenic) eggs and the number of terminal

* Each data point represents the average egg number of the population sample dissected for any given week.

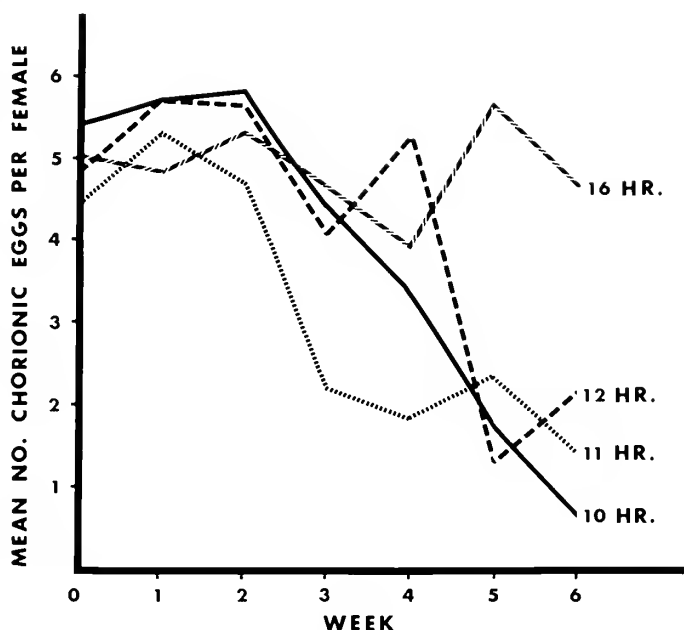


Fig. 1B. The influence of photoperiod on the average number of chorionic eggs in *B. intermedia*.*

oocytes which were larger than 0.33 mm in length were recorded. The final stages of oocyte resorption were characterized by the disappearance of lipid yolk spheres. In order to characterize more fully the state of oocyte development, ovaries dissected in the 10 hr and 16 hr photophase experiments (see below) were stained with trypan blue for 20 minutes at 23°C (Telfer and Anderson 1968). This dye is an accurate index of the change from normal vitellogenesis to oosorption, based on alteration of the oocyte membrane.

Week numbers refer to the number of weeks in which the wasps were kept under experimental conditions. Experiments were conducted in environmental control chambers which provided 50% R.H. and photoperiods and temperatures appropriate to each set of experiments.

To demonstrate the influence of photoperiod on oosorption, adults were exposed to 21.1°C and the following photophases: 10, 11, 12, 16 hr. The influence of exposure to short photoperiod prior to adult reproductive maturity was also investigated. Wasps were reared in their pupal host and kept after adult parasitoid emergence for 2 weeks in a 12 hr photophase and 21.1°C and compared to those kept in a 16 hr photophase and 21.1°C for the same period. Finally, three cohorts of adults were kept each at an 11 hr

* Each data point represents the average egg number of the population sample dissected for any given week.

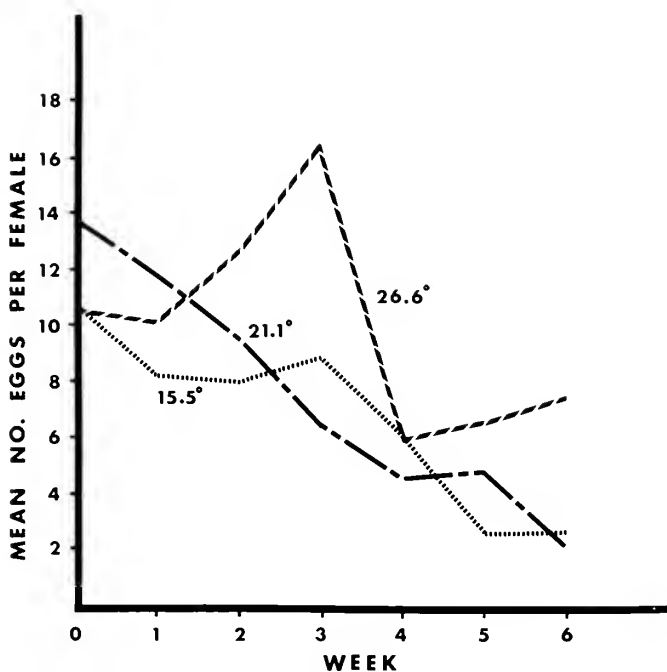


Fig. 2. The influence of temperature on the average number of vitellogenic eggs in *B. intermedia*.*

photophase and at 15.5°C, 21.1°C or 26.6°C to investigate temperature effects on oosorption.

Analyses of variance and Duncan's new multiple range tests were performed to determine significant differences in the data.

Results and Discussions

Oosorption in *B. intermedia* is affected by photoperiod. (Figs. 1A, B). That oosorption ensued in adults placed in a short photophase (10, 11, 12 hr) compared to those in long photophase (16 hr) is demonstrated by the decreasing egg numbers through the six weeks of the experiments ($P < 0.01$). Adults kept in a long photophase showed a less dramatic decline in oocyte number compared to short photophase (10, 11 and 12 yr). The overall trend in total number of oocytes (Fig. 1A) is similar to that of number of chorionic eggs (Fig. 1B). This concurrence is found in all subsequent experiments and thus, no other data on chorionic eggs are presented. From

* Each data point represents the average egg number of the population sample dissected for any given week.

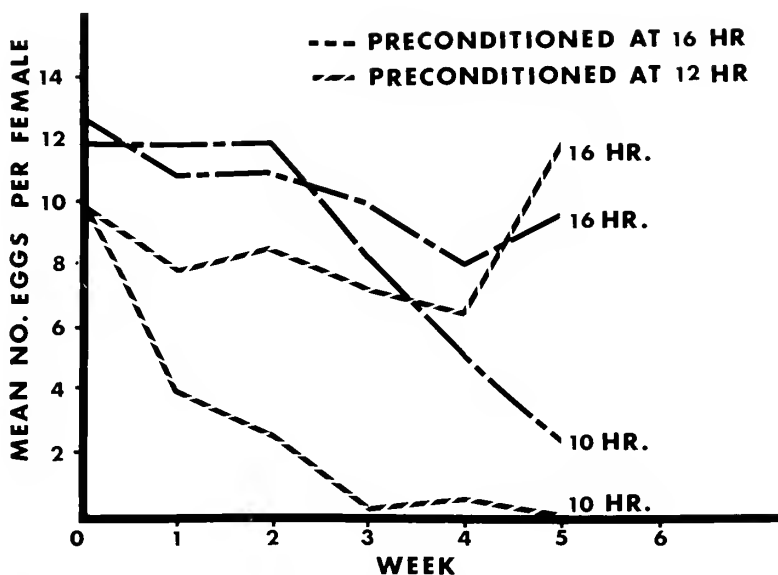


Fig. 3. The influence of photoperiod on the average number of vitellogenic eggs in immature and young adult *B. intermedia* (<2 weeks old.)*

weeks 0 to 6 the relationship between treatment means, for any given week, varies. This is due, in part, to the fact that weekly dissections necessitate the use of a new cohort of adults each week.

Adult female parasitoids have been reported to partially absorb eggs in the absence of hosts (Flanders 1950). Although greater resorption has been observed in older females, no quantitative study of the effect of age on resorption is yet available (Bell and Bohm 1975). Thus, although age (6 weeks) and absence of hosts may enhance oosorption, short photoperiod does have a direct effect on oosorption since adults at long photoperiod were of comparable age and they experience a similar lack of hosts in our experiments.

Low temperatures enhanced the effect of short photophase (Fig. 2). Oocyte resorption proceeded more quickly at lower temperatures as indicated by comparison of mean values at each temperature ($P < 0.01$). This is significant, particularly, since physiological processes generally advance more rapidly at higher temperatures.

The two series of experiments discussed above demonstrate the sensitivity of 2-week and older females to photoperiod and temperature. Exposure

* Each data point represents the average egg number of the population sample dissected for any given week.

of immature stages of *B. intermedia* (within its host) and of young adults (<2 weeks old) to short daylength had marked consequences on their ovarian development (Fig. 3). Adults preconditioned at a 12 hr photophase before being placed in a 10 or 16 hr photophase generally had fewer oocytes with yolk at week 0 than those preconditioned at a 16 hr photophase ($P < 0.01$). Those adults placed in a short photophase (10 hr) had totally resorbed ovaries laden with fatty tissues by week 5. Those placed in long daylength (16 hr) maintained a higher mean no. of eggs per female compared to adults in a short photophase.

Females are the overwintering stage of *B. intermedia*. Short-day photoperiods and low temperatures characterize pre-overwintering conditions, when few, if any, hosts are available to *B. intermedia*. Oosorption of oocytes under these conditions (short photophase and low temperature) would represent a logical adaptive mechanism to conserve nutrients critical to the overwintering (diapausing) female. Indeed in 1942, Flanders stated that in the parasitic Hymenoptera the occurrence of oosorption is an adaptation for maintaining the reproductive capacity when environmental conditions are unfavorable for oviposition.

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BOOK REVIEW

C. L. Mandahar. *Introduction to Plant Viruses*. 333 p. 1978. S. Chand & Co., Ltd., New Delhi. 20 rupees (\$3.00).

This book contains 13 chapters on subjects relating to plant viruses. A brief, interesting introduction presents the discovery of viruses, their nature, and hypothesis of their origin. A chapter on isolation and purification gives a description of methods and contains useful information on salient features of virus concentration and purity. An entire chapter is devoted to modern tools and techniques, such as the electron microscope, X-ray diffraction, fluorescent antibody technique, animal and plant tissue culture, as well as assays with indicator plants. Virus structure and chemistry are well presented and illustrated. Current knowledge on multicomponent, incomplete, and satellite viruses is brought up to date. Other chapters deal with disease symptoms, translocation and distribution, infection and replication, and variability. Entomologists will be most interested in the chapter dealing with transmission. Here the author discusses in detail the various groups of vectors, such as aphids, leafhoppers, whiteflies, mealybugs, beetles, and others, and the interactions between plant viruses and vectors. Harmful and beneficial effects on arthropod transmitters, transovarial transmission, and vector specificity are all expertly described. A separate chapter is devoted to virus nomenclature and classification. The recently discovered spiroplasma and mycoplasma-like agents of plant diseases are also included, since they were earlier considered as plant viruses. The last chapter concerns various methods used to control plant virus diseases. A subject index and author index are provided. In addition to text illustrations, there are 28 pages of figures, containing electron micrographs of viruses, quite well reproduced on glossy paper.

This is a very useful book, in which each section is up-to-date. The chapters are relatively free of errors, and provide a concise but thorough source of information. This hard-cover book can be recommended as a text for graduate students in agricultural colleges and universities. It is authoritative and at its price a real bargain! It might also find its way, as a source of information on plant viruses, to public libraries and it certainly belongs to private libraries of plant virologists and plant pathology teachers.

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BOOK REVIEW

Biochemistry of Insects. Morris Rockstein, ed. Academic Press. 649 p. 1978. \$29.50.

This volume consists of 14 chapters, covering all aspects of insect biochemistry, the protein synthesis, insect pigments, cuticle, chemical genetics and the functional role of carbohydrates. The authors of this treatise are among the leading authorities in the diverse areas of insect biochemistry. G. Michael Chippendale gives an in-depth analysis of the function of carbohydrates in insect life processes. Roger G. H. Downer discusses the fundamental role of lipids, their digestion, transport, biosynthesis and endocrine regulation of lipid metabolism. Moises Agosin covers the functional role of proteins, and P. S. Chen protein synthesis in relation to cellular activation and deactivation. The insect cuticle, sclerotization and melanization are the subject of a chapter by A. Glenn Richards. The role of insect biochromes is presented by A. E. Needham. Lynn M. Riddiford and her husband James W. Truman combined forces to give a lucid and stimulating presentation of the present status of insect hormones and growth regulators. Nevin Weaver covers the intraspecific chemical control of behavior, while Wendell L. Roelofs deals with pheromones. The biochemical defenses are the subject of Muray S. Blum's exciting presentation. R. D. O'Brien gives an up-to-date analysis of the biochemistry of toxic action of insecticides. The detoxication mechanisms are described by W. C. Dauterman and Ernest Hodgson. The last chapter, by Francisco J. Ayala, is on chemical genetics and evolution.

Each chapter includes a general reference list of pertinent books and reviews for advanced students and research scientists. There is an extensive subject index. The volume is unique in providing an authoritative and comprehensive coverage of a critical interdisciplinary area. The quality of the contributions is uniformly high and exceptionally stimulating. The contributors covered thoroughly all aspects of insect biochemistry and thus provided a volume that will be indispensable for researchers, students, and teachers and will have lasting value. This outstanding book will be of interest to workers in entomology, agriculture, toxicology, pesticides, bio-organic chemistry, pollution research, ecology, and biochemistry.

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BOOK REVIEW

The Life that Lives on Man. By Michael Andrews. Toplinger Publishing Co., New York. 183 p. 1976. Paperback \$4.95; cloth \$9.95.

This is a delightful book, and its selection by Library Journal as one of the 100 best science books of 1977 certainly seems justified. The "life"

includes viruses, bacteria, yeasts, as well as mites, ticks, fleas, lice and bed bugs that live on our skin. The author has a good sense of humor as well as the ability to present the subject matter in a very readable manner. Illustrations include numerous scanning electron micrographs and excellent photographs of, among others, delousing, antityphus squads, and drawings of various insects. The photograph of the Apollo 12 on the moon illustrates the revealing finding by Surveyor III astronauts and Houston scientists that the camera, which had spent 2 years on the moon's surface, was still contaminated with bacteria from earth. Although this book is written for the layman, it will be of considerable interest to professional entomologists as well as to teachers and students in entomology departments. The book belongs in personal and institutional libraries, as well as in public libraries.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers University.*

BOOK REVIEW

Introduction to Insect Biology and Diversity. By Howell V. Daly, John T. Doyen, and Paul R. Ehrlich. McGraw-Hill Book Co. 564 p. 1978. \$19.50.

This handsome volume is a novel and modern approach to an introductory text in entomology. It is intended for students who have completed a basic course in biology. The lectures are devoted to insect structure and function, ecology, behavior, and applied aspects. There are keys for insect identification and the combined volume provides a foundation for professional entomological training. The first part of the book deals with insects as organisms and the excellent illustrations help the beginner to digest the complex nature and diversity of insects. The second part on population biology follows an earlier book by Erhlich et al. (1974), giving a description of the evolutionary mechanism underlying the great variability of insects. The third part discusses insects in relation to the environment: insects of soil and water, relation of insects to plants, vertebrates, microbes and helminths, as well as biotic and physiological factors of the environment. The fourth part deals with insect diversity. A glossary, a list of references, and a taxonomic and subject index complete the volume. Throughout the book, discussions of biological phenomena are cross-referenced to more detailed treatments in various parts of the volume. Although the book has been written by three authors, it gives a uniform impression of a single-authored text. The photographs, credited to a large number of renowned entomologists, are all excellent, and it can be expected that many teachers of introductory entomology will adapt this text for their courses. Occasionally the book departs from the traditional boundaries of entomology, but the final result is most

satisfactory. There has been a need for a modern, stimulating entomology text and the authors are to be congratulated for preparing this impressive, modern, up-to-date introductory volume.

Karl Maramorosch, *Waksman Institute of Microbiology, Rutgers University*.

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DR. CHARLES PAUL ALEXANDER

Charles Paul Alexander was born in Gloversville, New York, September 25, 1889, the son of Emil and Jane Parker Alexander. He entered Cornell University in 1909 to study entomology and received the Bachelor of Science degree in 1913, and the Doctor of Philosophy degree in 1918. While a student, he served as assistant, and later as instructor, in general biology and natural history. He was curator of the Snow Entomological Collection of the University of Kansas from 1917 until 1919. At the Illinois State Natural History Survey, Urbana, he served as curator of the insect collections from 1919 until 1922. In 1922, he went to the then Massachusetts Agricultural College as assistant professor of entomology. He assumed charge of entomology in 1930 and was named chairman of the Department of Entomology and Zoology in 1938. He was Acting Dean of the School of Science from 1945 until 1946, when he was appointed Dean, a position he held until 1952. He retired from active teaching in 1959.

Charles P. Alexander is a Fellow of the American Association for the Advancement of Science and a member of many leading entomological societies in the United States and abroad. He is an Honorary Member of the New York Entomological Society. In 1942 and 1943, he served as president of the Entomological Society of America.

In 1917, he married Mabel M. Miller of Brookview, New York. She has been his constant companion and helper, collecting insects, doing all the driving on field trips, and coauthoring papers.

Charles P. Alexander is probably best known as an authority on one of the largest groups of insects, the crane flies (Diptera: Tipulidae). His interest in the group started in 1906, when he visited Dr. E. P. Felt, the state entomologist of New York, for help in identifying some specimens of crane flies. The very conspicuous species were easily identified, but there was no one available to identify the rest. Encouraged by Drs. James G. Needham and Charles W. Johnson, who assured him that the family was ripe for study, Alexander has been studying the crane flies to this day. He has collected crane flies regularly and widely. The lure of opportunities for crane fly collecting has always been strong, and many field trips were taken, some as far as Alaska. A typical western trip covered more than 10,000 miles, lasted 80 days, and resulted in the collection of about 5,000 crane flies and more than 25,000 other insects for the University of Massachusetts collections. He has assembled what is probably the most complete collection of any major group of insects. It includes almost 13,000 species of crane flies, many represented by type material, acquired from museums, collectors, expeditions, and his own field trips. Of particular importance is a reference collection of more than 50,000 microscope slides showing the various struc-



Dr. Charles Paul Alexander, 1950.

tures needed in taxonomic study of the group. Alexander has described over 10,000 species of tipulids and published more than 1,000 papers on them.

After his retirement from active teaching, he transferred his crane fly collection to his home in Amherst, Massachusetts, where he had a special annex built to contain the collection. In "Crane-fly Haven," as this annex is known, Alexander has continued his entomological research free from academic responsibilities. With his comprehensive knowledge and incomparable collection of tipulids, he has accomplished a tremendous amount of taxonomic work in a relatively short time. But as he realizes perhaps more than anyone else, knowledge of crane flies is still incomplete. Despite his work in taxonomy, the majority of species are represented only by adults,



Dr. Alexander in "Crane-fly Haven," Amherst, Massachusetts. Top left: With reprints of his publications. Top right: At work. Bottom left and right: Charles and Mabel Alexander, 1979.

and little is known about the ecology, behavior, and biology of all stages of most of the species. However, few other groups have such a strong taxonomic foundation upon which to build.

In recognition of this great entomologist's intensive efforts and impressive accomplishments over the past 68 years, this issue of the *Journal of the New York Entomological Society* is dedicated to Dr. Charles Paul Alexander on his 90th birthday.

Dr. Henry M. Knizeski, Jr., Department of Natural Sciences, Mercy College, Dobbs Ferry, New York 10522.

KEYS AND DIAGNOSES FOR THE FAMILIES OF WESTERN
HEMISPHERE PENTATOMOIDEA, SUBFAMILIES OF
PENTATOMIDAE AND TRIBES OF PENTATOMINAE
(HEMIPTERA)

L. H. Rolston and F. J. D. McDonald

Abstract.—The families of Pentatomoidea of the Western Hemisphere (Acanthosomatidae, Canopidae, Corimelaenidae, Cydnidae, Cyrtocoridae, Dinidoridae, Megarididae, Pentatomidae, Phloeidae, Scutelleridae, Tessaratomidae), the subfamilies of Pentatomidae (Asopinae, Discocephalinae, Edessinae, Pentatomini, Podopinae), and the tribes of Pentatomini (Halyini, Mecideini, Pentatomini, Sciocorini) are keyed and diagnosed. Edessinae is raised from tribal status and *Pantochlora* Stål included in this subfamily. All Western Hemisphere genera formerly included in Halyini except *Brochymena* Amyot and Serville are removed from this tribe. *Caracia* Stål, *Marghita* Ruckes and *Janeirona* Distant are transferred to Pentatomini. *Janeirona* is a senior synonym of *Zimmerana* Ruckes.

Identification and classification of many pentatomoids of the Western Hemisphere have been hampered by the lack of a recent conspectus of the taxon. This contribution to such a conspectus may resolve some difficulties.

Our opinions regarding the classification of Western Hemisphere pentatomoids are based on study of the external morphology and genitalia. The genital structure of suprageneric taxa has been characterized when sampling for dissection was sufficiently broad that generalizations could be drawn with confidence, and when such generalizations seem useful in defining a taxon.

We consider 11 taxa of the pentatomoids represented in the Western Hemisphere to merit family rank: Acanthosomatidae, Canopidae, Corimelaenidae, Cydnidae, Cyrtocoridae, Dinidoridae, Megarididae, Pentatomidae, Phloeidae, Scutelleridae, and Tessaratomidae. This classification is traditional, although the canopids, corimelaenids, and megaridids are sometimes regarded as subfamilies of the cydnids. These 4 taxa were treated as subfamilies of the Pentatomidae by McAtee and Mallock (1928, 1933) in the most recent revision of the megaridids, canopids, and corimelaenids. However, the Pentatomidae in the classification of the above authors is equivalent to the Pentatomoidea as currently understood, and their subfamilies should be valued in context. Froeschner (1960) also excluded the canopids, corimelaenids, and megaridids from the cydnids in his revision of the Cyndidae of the Western Hemisphere. Kormilev (1955) argued eloquently in favor

of family status for the cyrtocorids but did not formally elevate the taxon from subfamily rank.

We recognize 5 subfamilies of Pentatomidae in the Western Hemisphere: Asopinae, Discocephalinae, Edessinae, Pentatominae, and Podopinae. The conspicuous departure from the usual classification is the elevation of the Edessinae from tribal status. The genus *Pantochlora* Stål, ejected by Kumar (1969) from the Tessaratomidae, is included in the Edessinae.

The Pentatominae of the Western Hemisphere have long been distributed among the tribes Halyini, Mecideini, Pentomini, and Sciocorini. No reason appears for disturbing this arrangement. We are not in accord with a proposal by Leston (1957) to raise the Mecideini to subfamily rank.

Key to Families of American Pentatomoidea

- | | |
|--|----------------|
| 1. Scutellum covering most of fore wings (Fig. 1) | 9 |
| – Scutellum leaving most of fore wings exposed even when scutellum attains apex of abdomen (Fig. 2) | 2 |
| 2. Scutellum bearing large mesial spine or vertical plate | Cyrtocoridae |
| – Scutellum not so armed | 3 |
| 3. Metathoracic scent gland orifice near lateral margin of pleuron (Fig. 3); antennae 3-segmented | Phloeidae |
| – Metathoracic scent gland orifice distant from lateral margin of pleuron; antennae 4- or 5-segmented | 4 |
| 4. Each pair of trichobothria on sternites iii–vii* on large callus located mesad of adjacent spiracle | Dinidoridae |
| – Trichobothria not on large callus, both (if paired) rarely mesad of spiracles on all sternites | 5 |
| 5. Pronotum extending over base of scutellum | Tessaratomidae |
| – Pronotum ending at base of scutellum | 6 |
| 6. Tibial spines if present confined to apex of tibiae | 7 |
| – Tibiae bearing many spines in addition to those at apex of tibiae and in addition to setae | 8 |

Fig. 1. *Chelysoma scurrilis*. Dorsum.

Fig. 2. *Moncus obscurus*. Dorsum.

Fig. 3. *Phloea subquadrata*. Scent gland orifice (s.a).

Fig. 4. *Ditomotarsus punctiventris*. Terminal segments of male abdominal venter: sternite viii; pygophore (py).

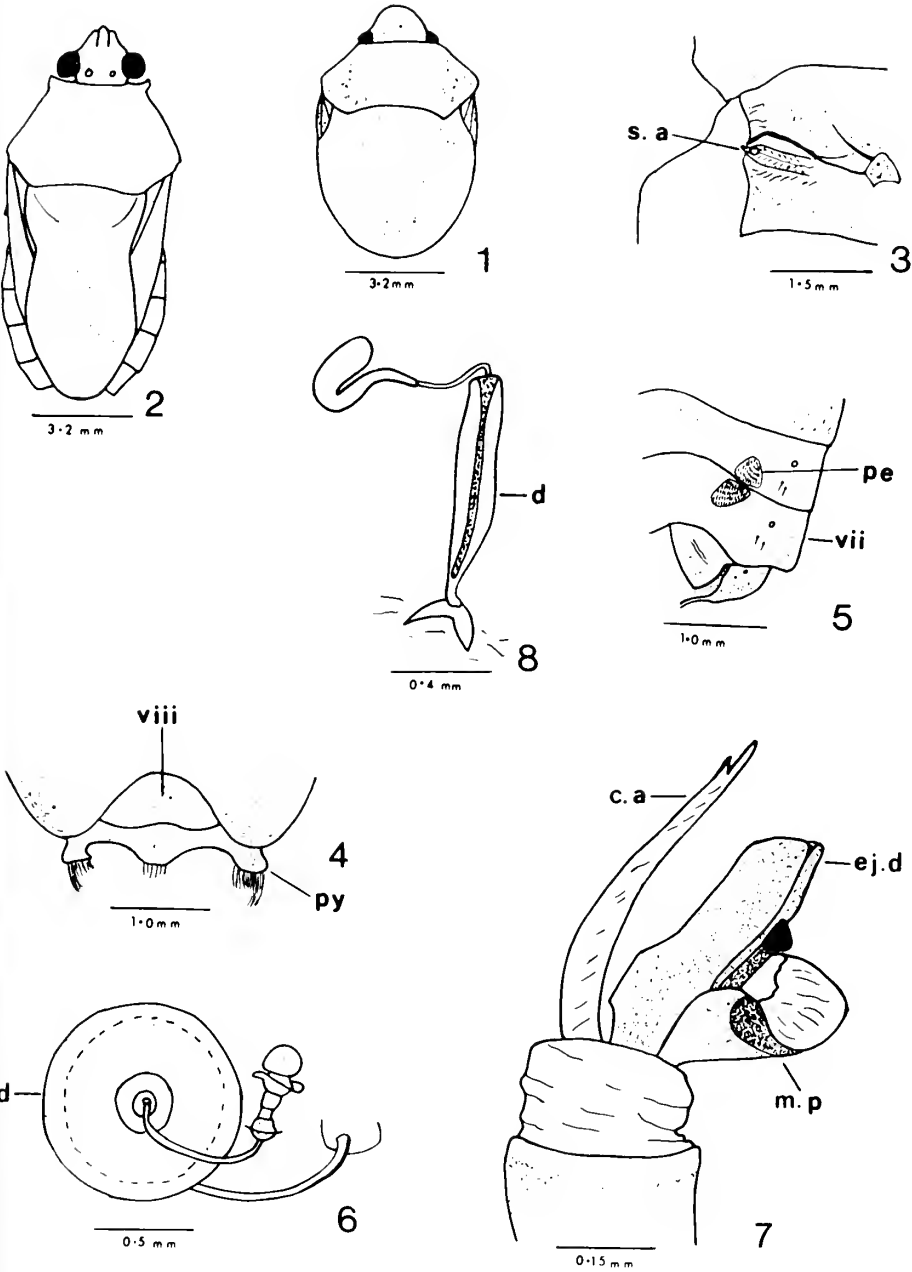
Fig. 5. *Planois gayi*. Pendergrast's organs (pe).

Fig. 6. *Canopus burmeisteri*. Spermatheca: spermathecal dilation (d).

Fig. 7. *Canopsis orbicularis*. Aedeagus: median penial lobe (m.p); ejaculatory duct (ej.d); conjunctival appendage (c.a).

Fig. 8. *Cyrtocoris* sp. Spermatheca: spermathecal dilation (d).

* Sternite ii is the first visible sternite.



7. Sternite viii exposed in males (Fig. 4); Pendergrast's organs usually present in females (Fig. 5); tarsi 2-segmented Acanthosomatidae
 - Sternite viii concealed in males; Pendergrast's organs absent in females; tarsi usually 3-segmented Pentatomidae
8. Fore tibiae usually expanded, sometimes cultrate with tarsi inserted midway of length, bearing lateral row of especially stout spines unless cultrate; apex of scutellum usually narrowly rounded
Cydnidae
 - Fore tibiae subcylindrical, spines on lateral margin not notably larger than others; apex of scutellum broadly rounded Corimelaenidae
9. Tarsi 2-segmented Megarididae
 - Tarsi 3-segmented 10
10. Tibiae bearing many spines in addition to those at apex and in addition to setae, if weakly spined lateral margins of pronotum fringed with long setae Corimelaenidae
 - Tibial spines if present confined to apex 11
11. Sutures of abdominal venter complete, reaching lateral margins; second antennal segment much longer than diameter 12
 - Sutures of abdominal venter obsolete laterad of spiracles; length of second antennal segment subequal to diameter Canopidae
12. Trichobothria paired; frena lacking Scutelleridae
 - Trichobothria single; short frena present Pentatomidae

Acanthosomatidae Signoret, 1863

Acanthosomites Signoret, 1863, p. 549.

Tarsi 2-segmented. Sternite viii exposed in males (Fig. 4). One or 2 pairs of Pendergrast's organs usually present in females, these depressed, round or elongate, located laterally on sternites v–vii, vi–vii or sternite vii only, a single depression often extending across more than one sternite (Fig. 5). Scutellum subtriangular, about half or less than half as long as abdomen; frena extending along at least basal 7 tenths of lateral margins of scutellum.

The genera of the Western Hemisphere were keyed by Rolston and Kumar (1974) and the family was revised by Kumar (1974).

Canopidae Amyot and Serville, 1843

Canopides Amyot and Serville, 1843, p. 70.

Canoparia Horvath, 1919, p. 205.

Scutellum covering most of fore wings, leaving little more than exocorium exposed except at base. Tibiae setose but lacking stout spines. Sutures between abdominal sternites obsolete laterad of spiracles. Tarsi 3-segmented. Antennae 5-segmented; second segment subequal to its diameter. Body obovate, strongly convex, shiny black.

Dilation of spermathecal duct discoidal. Spermathecal pump well developed (Fig. 6). Conjunctival appendages of aedeagus well developed. Median penial lobes fused into trough beneath ejaculatory duct (Fig. 7).

Canopus Fabricius, the only genus in this entirely American family, was revised by McAtee and Malloch (1928).

Corimelaenidae Uhler, 1872

Corimelaenidae Uhler, 1872, p. 471.

Thyreocoridae Van Duzee, 1907, p. 5.

Eucoriinae Sailer, 1945, p. 133.

Scutellum covering most of fore wings, leaving little more than exocoria exposed except basally, or U-shaped, broadly rounded apically, leaving most of fore wings exposed. Fore tibiae neither notably expanded nor cultrate; tibiae bearing in addition to setae numerous spines along length; if only hind tibiae spined and weakly so, then coria and lateral margins of pronotum fringed with long setae. Anterior margins of middle and hind coxae bordered with dense fringe of short setae. Reticulation of eyes not attaining ventral surface of head. Tarsi 3-segmented. Antennae 5-segmented.

In their revision of the corimelaenids, McAtee and Malloch (1933) recognized 9 genera, all from the Western Hemisphere except one monotypic genus.

The structure of the spermatheca and male genitalia varies considerably among genera of corimelaenids, suggesting that further consideration should be given to the suprageneric classification of this family.

Family name.—There has been no concensus of opinion on the name of this family, and both Corimelaenidae and Thyreocoridae have been widely used. We believe that Corimelaenidae is the appropriate family name.

Thyreocorides was proposed by Amyot and Serville (1843) as a supra-generic name for 6 genera (*Chlaenocoris*, *Coptosoma*, *Heterocratis*, *Plataspis*, *Strombosoma* and *Thyreocoris*). However, 7 of the 9 species listed under these genera are plataspids, including the 2 species assigned by Amyot and Serville to *Thyreocoris*: *T. coccinelloides* (Lap.) and *T. punctatus* (Leach). Another species is a canopid (*Canopus impressus* (Fabricius) = *Chlaenocoris impressus*). McAtee and Malloch (1933) left the remaining species, *Strombosoma unipunctatum* Amyot and Serville, unclassified although admitting its affinity to "Thyreocorinae." The principal corimelaenid genera, *Corimelaena* and *Galgupha*, were placed by Amyot and Serville with the scutellerid genus *Odontoscelis* under their supra-generic name *Odontoscelides*. It would seem therefore that *Thyreocorides* Amyot and Serville should be regarded as a synonym of *Plataspidae* since the majority of the

included species are of this family. Certainly it has little or no relevance to the corimelaenids.

Corimelaenidae was introduced casually by Uhler (1872) in connection with notes on *Galgupha nitiduloides* (Wolff) and *Corimelaena extensa* Uhler, both of which he placed in the latter genus. Nevertheless, Uhler's concept of the family clearly included its 2 large genera, and there is no evidence that it extended beyond the present concept of the family. Corimelaenidae appears to be the first family-group name relevant to this taxon that has been widely accepted.

The argument for using Corimelaenidae for this taxon pivots on whether or not Thyreocoridae has been "generally accepted by zoologists interested in the group concerned," a necessary requisite for availability (under Article 11 (e) iii of the International Code of Zoological Nomenclature) of family-group names originally published before 1900 and subsequently fully latinized. The persistence of a dual nomenclature for this family indicates to us the lack of general acceptance of Thyreocoridae, and the reason that this name should not become preeminent we believe to be compelling.

Cydnidae Billberg, 1820

Cydnides Billberg, 1820, p. 70.

Fore tibiae with row of stout spines along lateral margins, usually expanded, or cultrate with tibiae inserted midway of length. Middle and hind coxae thickly fringed with short setae along anterior margins. Reticulation of eyes reaching ventral surface of head. Scutellum exposing nearly all of fore wings. Tarsi 3-segmented, sometimes absent on hind legs. Antenna 4- or 5-segmented.

Froeschner (1960) recognized 15 genera and 5 subfamilies in his revision of Western Hemisphere representatives of this family.

→

Fig. 9. *Cyrtocoris* sp. Aedeagus, lateral view: conjunctival appendage (c.a); ejaculatory reservoir (ej.r); ejaculatory duct (ej.d).

Fig. 10. *Cyrtocoris* sp. Aedeagus, ventral view: theca (t); conjunctival appendage (c.a); ejaculatory duct (ej.d).

Fig. 11. *Dinidor* sp. Spermatheca: accessory spermathecal dilation (a.d).

Fig. 12. *Dinidor* sp. Aedeagus, retracted: ejaculatory reservoir (ej.r); median penial lobe (m.p); ejaculatory duct (ej.d).

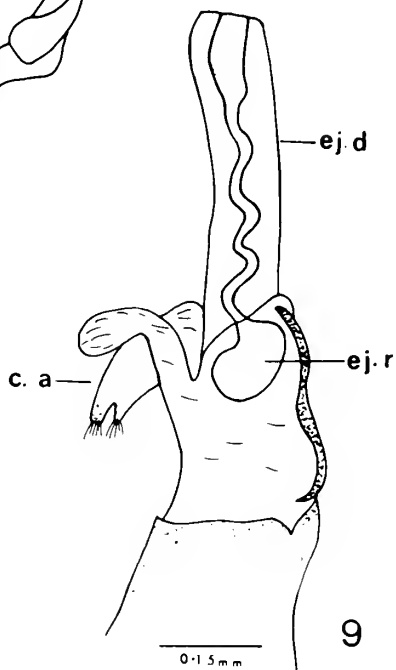
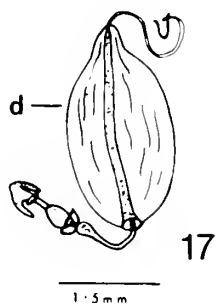
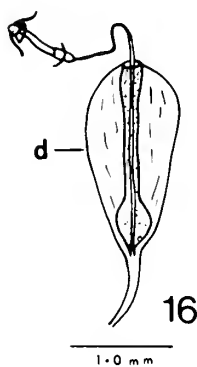
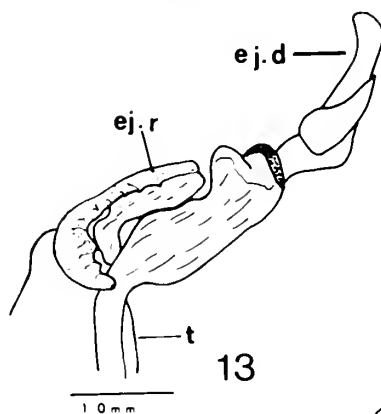
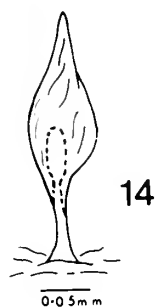
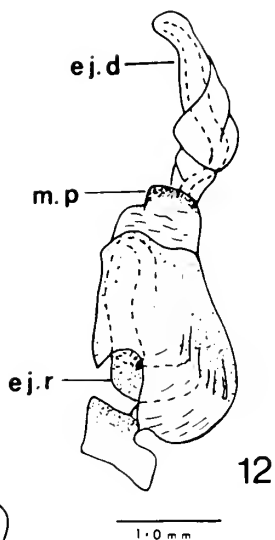
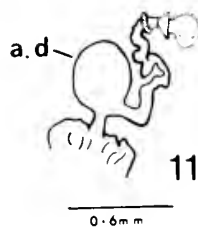
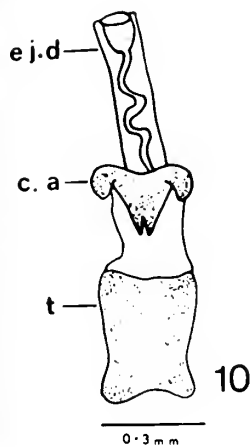
Fig. 13. *Dinidor* sp. Aedeagus, expanded: theca (t); ejaculatory reservoir (ej.r); ejaculatory duct (ej.d).

Fig. 14. *Megaris laevicollis*. Spermatheca.

Fig. 15. *Megaris constricta*. Aedeagus.

Fig. 16. *Alitocoris parvus*. Spermatheca: spermathecal dilation (d).

Fig. 17. *Edessa* sp. Spermatheca: spermathecal dilation (d).



Cyrtocoridae Distant, 1880

Oxynotides Amyot and Serville, 1843, p. 58. (part)

Cyrtocorinae Distant, 1880, p. 43.

Body covered with fine setae and waxy granules, the latter often fused. Scutellum extending to apex of abdomen, bearing mesial spine or vertical plate arising on basal half of scutellum and usually sloping dorsocaudad. Abdominal segments iii-vi projecting laterad well beyond coria, ii-v separated at lateral margins; sternites vi-vii laterally and genitalia nearly vertical. Tarsi 2-segmented. Antennae 5-segmented.

Spermatheca terminating in C-shaped bulb, without flanges or obvious pumping mechanism (Fig. 8). Ejaculatory duct of aedeagus large; channel small, sinuous, enlarged distally (Figs. 9, 10). Ejaculatory reservoir ever-sible. Conjunctival appendages present.

This wholly American family consists of 3 genera and 11 nominal species. Horvath (1916) revised the family and Kormilev (1955) added to this base in his treatment of the representatives occurring in Argentina.

Dinidoridae Stål, 1870

Dinidorina Stål, 1870, p. 79.

Coridiinae Schumacher, 1924, p. 335.

Each pair of trichobothria located on large callus mesad of spiracular line. Scutellum relatively small, about 4 tenths as long as abdomen, rounded apically. Antennae 4-segmented, distal 3 segments compressed, superior surface of segments 2 and 3 longitudinally impressed.

Spermathecal duct with globular side dilation basally. Spermathecal pump well developed (Fig. 11). Ejaculatory duct of aedeagus fairly voluminous, membranous, surrounded basally by median penial lobes (Figs. 12, 13). Conjunctival lobes apparently absent. Base of ejaculatory duct together with complex spermathecal reservoir completely ever-sible.

The above diagnosis applies only to the one American genus, *Dinidor* Latreille. Schouteden (1913), in his review of the world genera, listed 6 nominal species in *Dinidor*, one purportedly from Africa and the remainder from the Western Hemisphere.

Megarididae McAtee and Malloch, 1928

Megaridinae McAtee and Malloch, 1928, p. 1.

Body strongly convex, less than 5 mm long, usually less than 2 mm in length. Scutellum covering most of fore wings, coria little exposed except at base. Tarsi 2-segmented. Antennae apparently 4-segmented, with many setae as long as diameter of segments in female and much longer in male.

Spermatheca simple, saccular or globular (Fig. 14). Flanges and obvious pumping mechanism lacking. Aedeagus with membranous conjunctival lobes (Fig. 15). Ejaculatory duct tubular, simple.

McAtee and Malloch (1928) revised the single genus, *Megaritis* Stål, of this wholly American family. McDonald (1979) has reviewed the genitalia.

Pentatomidae Leach, 1815

Pentatomidae Leach, 1815, p. 121.

Scutellum leaving most of fore wings exposed, usually subtriangular, sometimes elongated and reaching apex of abdomen; disk flat, convex or gibbose basally. Pronotum terminating at base of scutellum. Tibial spines if present confined to apex. Tarsi usually 3-segmented, rarely 2-segmented. Trichobothria rarely located mesad of adjacent spiracle, if so not on large callus, usually paired but sometimes single. Metathoracic scent gland orifice distant from lateral margin of pleuron.

Dilation of spermathecal duct fusiform, membranous, with central invagination around sclerotized tube (Figs. 16, 17). Spermathecal pump usually well developed, with distal and proximal flanges and variously shaped bulb. Ejaculatory reservoir of aedeagus not eversible. Median penial lobes present, sometimes much expanded (Figs. 18, 19, 20). Conjunctival appendages usually present.

Key to Subfamilies of American Pentatomidae

1. Either first labial segment stout and extending well beyond bucculae, or fore tibiae foliate; pygophoral plate located entad of each paramere (Fig. 25) Asopinae
- First labial segment little enlarged, lying between bucculae (although often projecting beyond bucculae); fore tibiae not greatly expanded; pygophoral plate absent 2
2. Metasternum produced anteriorly onto mesosternum or rarely onto prosternum; rostrum not surpassing mesocoxae Edessinae
- Metasternum rarely produced anteriorly onto mesosternum, rostrum then extending onto abdomen; rostrum usually reaching at least to metacoxae 3
3. Trichobothrium nearest spiracle on sternite vii laterad of imaginary line tangential to spiracular openings on sternites vi and vii by distance at least equal to greatest diameter of spiracular opening (Fig. 26) 4
- At least one trichobothrium on sternite vii in or near imaginary band connecting spiracles and projected caudad of spiracle on sternite vii, or mesad of band 5

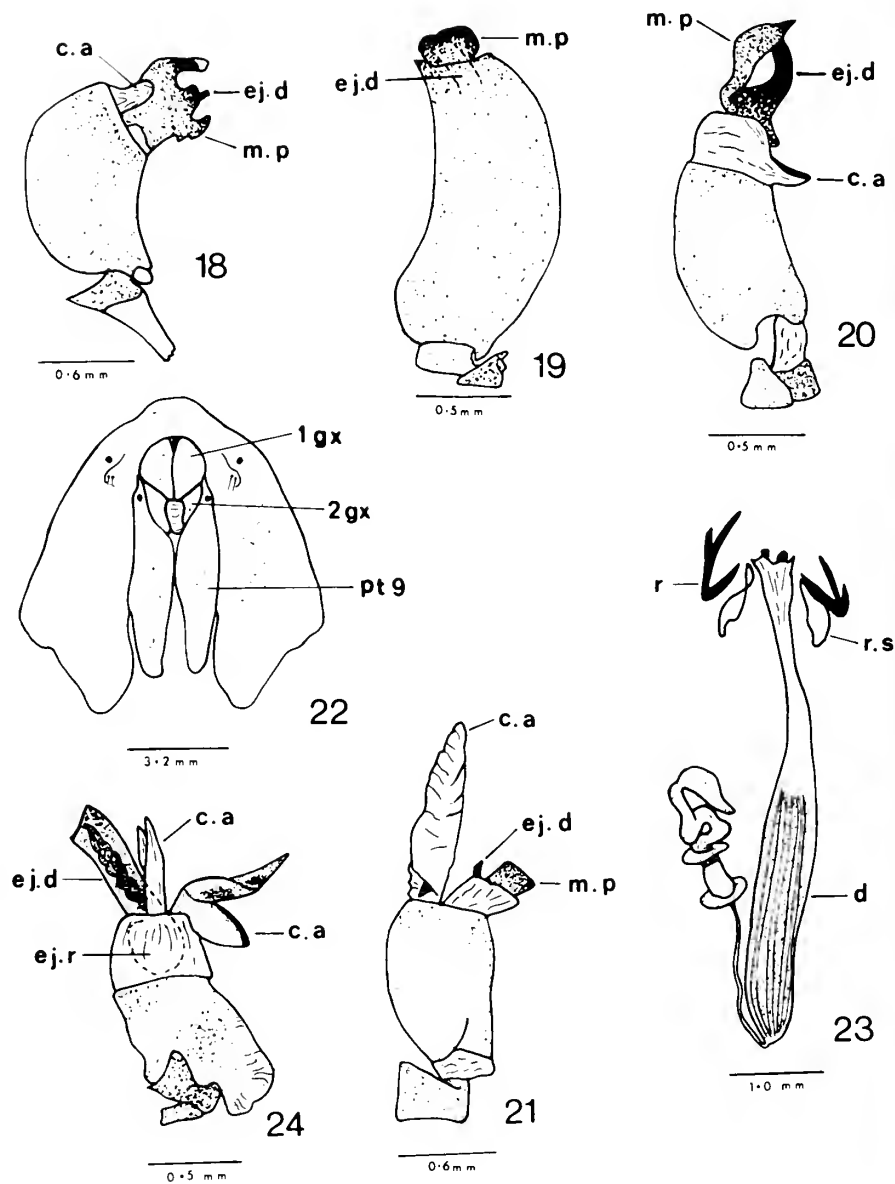


Fig. 18. *Uncinula tau*. Aedeagus: median penial lobe (m.p); ejaculatory duct (ej.d); conjunctival appendage (c.a).

Fig. 19. *Edessa* sp. Aedeagus: ejaculatory duct (ej.d); median penial lobe (m.p).

4. Base of abdominal venter with mesial tubercle and metasternum produced, flattened (in part) Pentatominae
- Abdominal venter rarely tuberculate at base, then metasternum thinly carinate mesially (in part) Discocephalinae
5. Labium arising on or behind imaginary line traversing head at anterior limit of eyes and/or superior surface of 3rd tarsal segment of hind legs shallowly excavated in females (in part) Discocephalinae
- Labium arising before such a line; superior surface of tarsal segments convex or flattened 6
6. Trichobothria single; frena short, less than one-third length of scutellum; scutellum reaching apex of abdomen Podopinae
- Trichobothria paired; frena one-third or more length of scutellum; scutellum not reaching apex of abdomen Pentatominae

Asopinae Spinola, 1850

Spissirostres Amyot and Serville, 1843, p. 74.

Asopoidae Spinola, 1850, p. 69 (1852). (Asopoideae intended.)

Amyotinae Schouteden, 1906, p. 1.

Arminae Bergroth, 1908, p. 180.

Cimicinae Kirkaldy, 1909, p. 1.

Pygophoral plate located entad of each paramere (Fig. 25). First labial segment usually stout and extending well beyond bucculae; if first labial segment of normal size and lying between bucculae for entire length, fore tibiae foliate. Males often bear pair of large pilose sensory patches, these usually extending across all or part of last 3 abdominal sternites. Tarsi 3-segmented. Antennae 5-segmented.

Schouteden (1906) revised the world genera and listed the nominal species then known of each.

←

Fig. 20. *Brochymena cariosa*. Aedeagus: conjunctival appendage (c.a); ejaculatory duct (ej.d); median penial lobe (m.p).

Fig. 21. *Halys neelgirensis*. Aedeagus: median penial lobe (m.p); conjunctival appendage (c.a); ejaculatory duct (ej.d).

Fig. 22. *Phloea subquadrata*. Genital plates: 9th paratergite (pt9); 2nd gonocoxae (2gx); 1st gonocoxae (1gx).

Fig. 23. *Phloea subquadrata*. Spermatheca: spermathecal dilation (d); ring sclerites (r.s); ramus (r).

Fig. 24. *Phloea subquadrata*. Aedeagus: ejaculatory reservoir (ej.r); conjunctival lobes (c.a); ejaculatory duct (ej.d).

Discocephalinae Fieber, 1860

Discocephalidae Fieber, 1860, p. 26.

Discocephalidum Stål, 1867, p. 499.

Labium usually arising on or posterior to imaginary line traversing head at anterior limit of eyes (Fig. 27). Trichobothria paired, one nearest spiracle on sternite vii usually laterad of imaginary band connecting spiracles and projected caudad of spiracle on sternite vii (Fig. 26). When labium arises before anterior limit of eyes, trichobothrium nearest spiracle on sternite vii laterad of spiracle by distance at least equal to greatest diameter of spiracular opening and/or superior surface of third tarsal segment of hind legs excavated in females. Metasternum not produced anteriorly onto mesosternum. Tarsi 3 segmented. Antennae 4- or 5-segmented.

Spermatheca typically pentatomid with central sclerotized tube in dilation of spermathecal duct and well developed pump (Fig. 16). Theca of aedeagus, ejaculatory duct, median penial lobes and conjunctival appendages (if present) heavily sclerotized, latter fused to margin of theca and permanently exerted (Fig. 18).

All American genera formerly included in the Halyini are removed from this tribe except *Brochymena*. Most of these genera will form a tribe of the Discocephalinae, but *Caracia* Stål, 1872, *Marghita* Ruckes, 1964, and *Janeirona* Distant, 1911 belong in the Pentatomini. The latter generic name is a senior synonym of *Zimmerana* Ruckes, 1962 (= *Zimmeria* Ruckes, 1958).

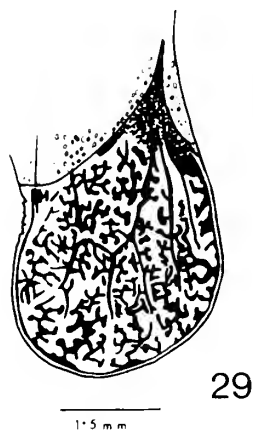
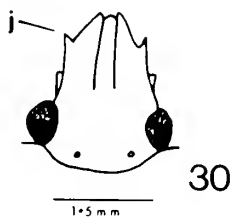
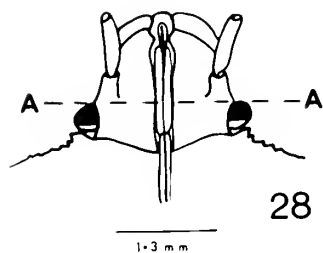
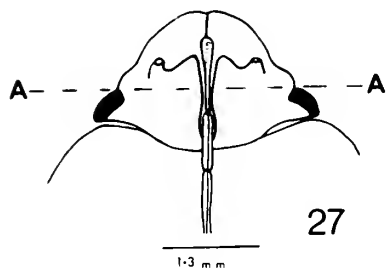
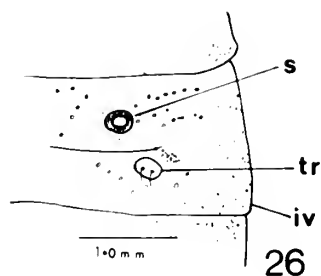
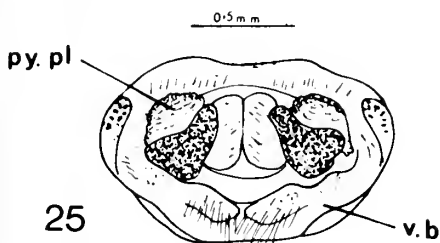
Edessinae Kirkaldy, 1909

Edessini Kirkaldy, 1909, p. 153.

Metasternum produced anteriorly onto mesosternum (onto prosternum in *Pantochlora*) and laterad between mesocoxae and metacoxae; posterior margin notched, receiving mesial tubercle of abdomen; anterior projection bifid (entire in *Pantochlora*). Rostrum terminating in anterior notch of metasternal projection (lying along projection in *Pantochlora*), reaching no farther than mesocoxae. Antennae 4- or 5-segmented. Tarsi 3-segmented.

Spermatheca typically pentatomid with central sclerotized tube in dilation of duct and well developed pump (Fig. 17). Theca elongated, slightly curved dorsoventrally (Fig. 19). Median penial lobes small, heavily sclerotized, surrounding short ejaculatory duct except ventrally. Conjunctive inconspicuous, sometimes apparent dorsally as small cone.

Pantochlora vivida Distant, the sole species in the genus, is not remarkably different from other members of the subfamily except in the form of the anterior metasternal projection. The genitalia, which Kumar (1969) has figured, conform to the diagnosis above.



- Fig. 25. *Podisus maculiventris*. Pygophore: ventral border (v.b); pygophoral plate (py.pl).
 Fig. 26. *Dryptocephala obtusiceps*. Abdominal sternite iv: trichrobothria (tr); spiracles (s).
 Fig. 27. *Discocephalessa humilis*. Ventral surface of head.
 Fig. 28. *Euschistus tristigmus*. Ventral surface of head.
 Fig. 29. *Brochymena quadripustulata*. Membrane of hemelytra.
 Fig. 30. *Brochymena parva*. Head, dorsal view.

Pentatominae Leach, 1815

Pentatomida Leach, 1815, p. 121.

Trichobothria paired, usually at least one of pair on each side of sternites iii-vii on or near imaginary band connecting spiracles on each side, pair rarely well mesad of spiracles. Metasternum rarely produced anteriorly onto mesosternum, if so rostrum reaching metacoxae. Basal segment of labium arising anterior to line traversing head at anterior margin of eyes, not especially stout, lying entirely between bucculae or distal end surpassing bucculae. Scutellum not attaining apex of abdomen, frena extending 4 tenths or more length.

Dilation of spermathecal duct fusiform, membranous excepting sclerotized rod around which dilation invaginates. Pump with proximal and distal flanges. Bulb spherical, digitiform or elongated and diverticulate. Conjunctival lobes usually large, usually bearing membranous appendages and sometimes sclerotized plates, in part or whole retractable into theca. Ejaculatory duct often extending beyond conjunctiva as sclerotized tube (penisfilum), this often looped or coiled.

Key to Tribes of Pentatominae

1. Abdominal venter with a longitudinal band of striations on each side extending across basal three or more segments Mecideini
- Striations absent on abdominal venter 2
2. Membrane of hemelytra bearing arborescent dark markings (Fig. 29); lateral jugal margins toothed preapically (Fig. 30) Halyini
- Membrane of hemelytra immaculate or with streaks or dots; jugal margins unarmed or with several small teeth 3
3. Lateral margins of pronotum explanate and second antennal segment at least 1.5 times length of third segment Sciocorini
- Lateral margins of pronotum rounded or carinate, if sublunate second antennal segment less than 1.5 times length of third segment Pentatomini

Halyini Dallas, 1851

Halydidae Dallas, 1851, p. 150.

Membrane of hemelytra with aborescent dark markings on frosty background (Fig. 29). Preapical tooth present on lateral margin of juga (Fig. 30). Patches of waxy secretion evident on venter. Mesial sulcus extending over several basal sternites on abdomen broad, shallow. Antennae 5-segmented.

In the Western Hemisphere only *Brochymena* Amyot and Serville is closely allied to *Halys* Fabricius. These two genera have similar features,

including the genitalia (Figs. 20, 21). Leston (1953a) suggested that the tribe Halyini might be defined on the basis of wax glands. Wax glands are not unique to the halyines, although they may be a common characteristic of the tribe.

Brochymena has been revised by Ruckes (1946).

Mecideini Distant, 1902

Mecidaria Distant, 1902, p. 140.

Abdominal venter with a longitudinal band of striations on each side extending across basal 3 or more segments. Body elongate, linear. Antennae 5-segmented, second segment triangular in cross-section.

The only mecideine genus in the Western Hemisphere, *Mecidea* Dallas, has been reviewed by Sailer (1952).

Pentatomini Leach, 1815

Pentatomidae Leach, 1815, p. 121.

Lateral margins of pronotum usually rounded or carinate from lateral view, if explanate second antennal segment less than 1.5 times length of third segment, usually subequal or shorter. Orifice of metathoracic scent gland often attended by elongate ruga, if auriculate auricle and evaporative area not sunken below metapleural surface. Antennae usually 5-segmented, occasionally 4-segmented.

Sciocorini Amyot and Serville, 1843

Sciocorides Amyot and Serville, 1843, p. 118.

Lateral margins of pronotum explanate. Second antennal segment at least 1.5 times length of third segment. Metathoracic scent gland opening auriculate, auricle and small evaporative area often sunken below surface of pleuron. Antennae 5-segmented.

Podopinae Amyot and Serville, 1843

Podopides Amyot and Serville, 1843, p. 56.

Graphosomini Jakovlev, 1884, p. 204.

Trichobothria single, one behind each spiracle in or near imaginary band connecting spiracles. Frena extending less than one-third length of scutellum. Scutellum reaching apex of abdomen, covering most of fore wings. Antennae 4- or 5-segmented. Tarsi 3-segmented. Pygophoral appendage (hypopygial appendage) often present, attached to posterolateral margin of pygophore.

Barber and Sailer (1953) revised the North American representatives of this subfamily.

Phloeidae Amyot and Serville, 1843

Phleides Amyot and Serville, 1843, p. 115.

Body extremely depressed; outer margins of juga, pronotum, coria basally and abdomen broadly foliate. Antennae and tarsi 3-segmented. Orifice of metathoracic scent gland near margin of pleuron (Fig. 3).

Ninth paratergites greatly elongated (Fig. 22). Dilation of spermathecal duct sclerotized, cylindrical, striated (Fig. 23). Pump well developed, bulb sinuous. Ring sclerites and sclerotized rami present within vulva. Ejaculatory reservoir of aedeagus eversible (Fig. 24). Channel of ejaculatory duct convoluted. Median penial lobes absent.

The family consists of two American genera, *Phloeophana* Kirkaldy and *Phloea* Lepeletier and Serville, and 3 species. Leston (1953b) monographed the family.

Scutelleridae Leach, 1815

Scutellerida Leach, 1815, p. 121.

Odontoscelidae Douglas and Scott, 1865, p. 13.

Eurygastridae Douglas and Scott, 1865, p. 13.

Scutellum leaving little of fore wings exposed except basally. Frena absent. Tibiae setose but without spines along length. Suture of abdominal venter extending to lateral margins. Antennae 5-segmented. Tarsi 3-segmented.

Schouteden (1904, 1906) revised the world genera and enumerated the nominal species then known of each.

Tessaratomidae Stål, 1865

Tessaratominae Stål, 1865, p. 33.

Pronotum projecting over base of scutellum. Metasternum produced laterad between coxae and cephalad onto mesosternum, most strongly produced as anterior wedge reaching nearly to procoxae, posterior margin transverse at junction with abdominal sternite. Six pairs of spiracles usually visible.

The only genus represented in the Western Hemisphere, *Piezosternum* Amyot and Serville, contains 3 species. The genitalia of this genus have been figured by Leston (1954), McDonald (1966) and Kumar (1969).

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POSITIONAL VARIATIONS AND MODIFICATIONS
RELATING TO THE PROTERGUM IN HYMENOPTERA

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Introduction

The present work is a part of a general research project concerned with the tracing of evolutionary trends related to various body features within the entire range of the order Hymenoptera. This work specifically includes observations dealing with the gradual changes in the position of the protergum, which in higher Hymenoptera shifts backwards to become closely associated with the anterior margin of the mesothorax. The extent and magnitude of this association varies, and these variations form a systematic graded pattern which cannot be without evolutionary significance. This study also throws some light on phylogenetic relations among the different families of this insect order. Thus far no comprehensive study has been undertaken indicating the succession of these changes which affects the thoracic topography in Hymenoptera. In 1910 Snodgrass recorded some observations pertaining to the changes in the hymenopterous thorax as a whole, but his observations were based on only eight families. The following authors also referred to this thoracic component, but without discussing the magnitude of its shift from any comparative angle: Snodgrass (1910, 1925), Bird (1926), Reeks (1937), Duncan (1939), Alam (1951), Arora (1953), Rivard (1955), Bracken (1961), Tait (1962), Wong (1963), Dhillon (1966) and Matsuda (1970). However, the present study which is based on observations made on the various hymenopterans belonging to about 20 different families of this insect order, does exactly this.

Summary

In Pamphiliidae and Xyelidae the protergum with its small antero-lateral angles is loosely attached to the mesotergum and the membranous areas prominently intervene between its posterolateral sides and the mesoepisternum. The protergum, however, in Tenthredinidae, Diprionidae, Argidae, Cimbicidae, Cephidae, Xiphydriidae and Siricidae is extended at its anterolateral angles and is rather more closely attached to the mesotergum. The above mentioned membranous areas are also considerably reduced. The chalcidoidea present further advancement in this trend, in which case the protergum is closely applied to the mesotergum and the membranous areas are mere interposing spots. In Ichneumonoidea the antero-lateral angles of the protergum are further extended antero-ventrally giving the pro-

tergum a collar-like appearance which on its postero-lateral sides abuts against the adjoining margin of the mesopectus thus leaving no trace of intervening membranous areas. A similar condition prevails in the males of Formicidae and Mutillidae, but in the females the protergum is secondarily fused with the mesotergum and mesopectus. Another line of modification is represented by Chrysididae, Scoliidae, Vespidae and Eumenidae, where, besides the considerable extension of the antero-lateral angles of the protergum, its postero-lateral angles also extend laterally in the form of spiracular lobes to cover the first pair of the spiracles. These modifications are further magnified in Sphecidae, in which the further extended antero-lateral angles of the protergum imparts to the latter an appearance of a pronounced collar. However, here the two opposite ends of the collar just touch but do not fuse. In Apoidea the opposite ends of the collar-shaped protergum fuse with each other and exist in the form of an entire annulus completely girdling the anterior margin of the mesothorax.

Material and Methods

To carry out the present study, most of the specimens of Apocrita were collected from the Punjab and Himachal Pradesh during the months of September and October 1975 and preserved in 80% alcohol. Symphyta, with the exception of Megalodontidae and Orussidae, were supplied by the Biosystematic Research Institute, Canada, and the Zoological Survey of India. As the specimens provided by them were dry, they were softened by immersion in 2% KOH for about 6 days. Diagrams were drawn with the help of a Stereoscopic microscope fitted with a graph eye-piece.

OBSERVATIONS AND DISCUSSION

(Figs. Plate I, II)

The sequential separation of the protergum from the propectus and its complete integration with the anterior margin of the mesothorax is a characteristic feature of the order Hymenoptera. This disassociation probably was initiated among the ancestors of the suborder Symphyta but it reached its climax in the higher apocritans where the protergum seems to be more an integral part of the mesothorax than of the prothorax. In the females of the families Formicidae and Mutillidae, the protergum is completely fused with the mesothorax and even the line of fusion is quite obscure. This fact reveals a trend of considerable evolutionary significance. An effort has been made to work out in sequence all the stages of the shift as represented in the position of the protergum vis-a-vis the propectus and the mesotergum in extant families.

The most primitive known condition is observed in the members of the families Pamphiliidae and Xyelidae. In *Acantholyda maculiventris* (Fig. 1)

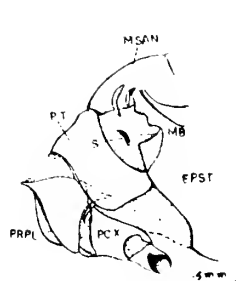


FIG. 1

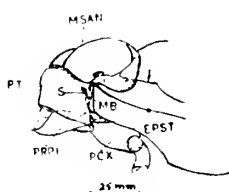


FIG. 2

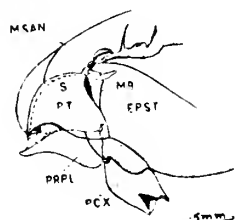


FIG. 3

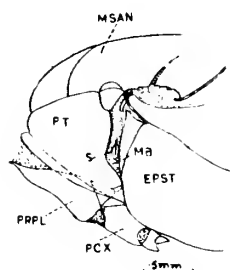


FIG. 4

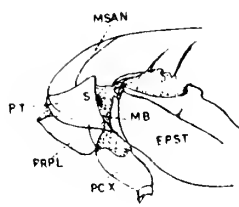


FIG. 5

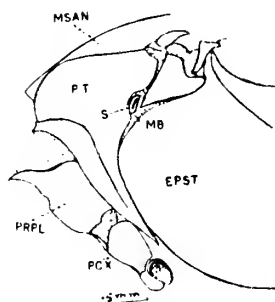


FIG. 6

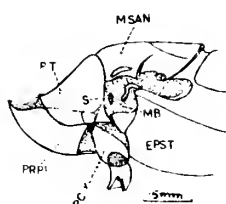


FIG. 7

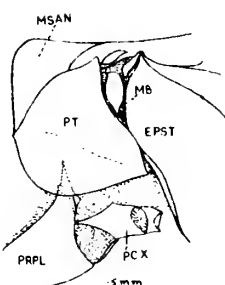


FIG. 8

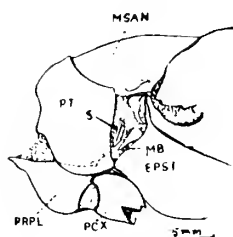


FIG. 9

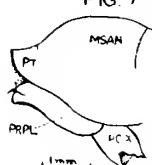


FIG. 34

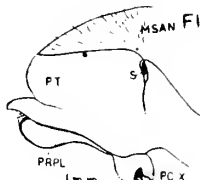


FIG. 35

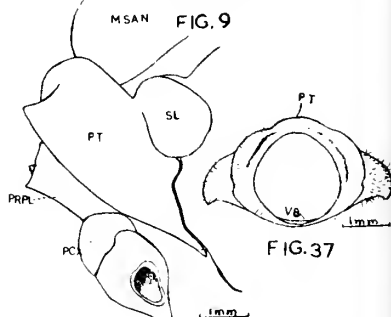
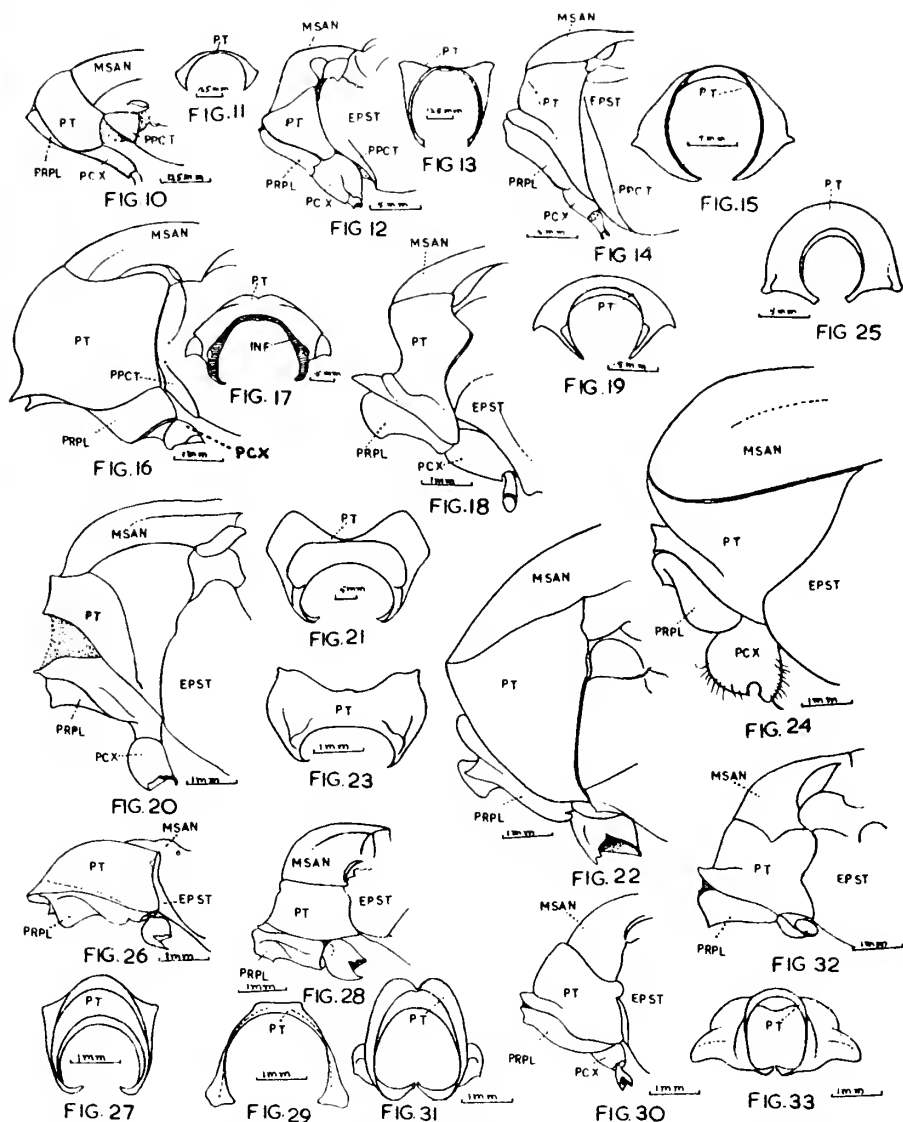


FIG. 36

FIG. 37

Side view of the protergum and its association with the mesothorax. 1. *Acantholyda maculiventris*; 2. *Xyela bakeri*; 3. *Neodiprion abietis*; 4. *Arge clavicornis*; 5. *Pristiphora cincta*; 6. *Cimbex americana americana*; 7. *Cephus (Cephus) cinctus*; 8. *Xiphydria mellipes*; 9. *Sirex cyaneus*; association of the protergum with mesothorax and the front view of the protergum:



10, 11. *Sycosapter stabilis*; 12, 13. *Netelia kashmirensis*; 14, 15. *Trachysphyrus* sp.; 16, 17. *Chrysis indogotea*; 18, 19. *Scolia quadripustulata*; 20, 21. *Vespa orientalis*; 22, 23. *Eumenes dimidiatipennis*; 24, 25. *Dorylus labiatus*; 26, 27. *Sina rufonigra*; 28, 29. *Camponotus camelinus*; 30, 31. *Scelephron intrudens*; 32, 33. *Stizus vespiformis*. Side view of the protergum and its association with the mesothorax; 34. female *Dorylus labiatus*; 35. female *Mutilla* sp.; association of the protergum with mesothorax and the front view of the protergum. 36, 37. *Xylocopa lemuiscapa*.

Abbreviations

EPST—Episternum; INF—Inflection; MSAN—Mesalinotum; MR—Membrane or (Membranous); PCX—Procoxa; PPCT—Prepectus; PRPL—Propleuron; PT—Protergum; S—Spiracle; SL—Spiracular lobe; VB—Ventral bridge.

(Pamphiliidae) and *Xyela bakeri* (Fig. 2) (Xyelidae) the protergum is weakly attached to the anterior margin of the mesonotum and also there are present membranous areas between its sides and the mesoepisternum. On the whole, the association of the pronotum with the mesothorax is not rigid and in this case it does not seem to be an integral part of the latter. A similar condition has also been observed in *Pamphilius luteicornis* and *Cephalcia provancheri* (Pamphiliidae). These observations are further substantiated by the similar work of Rivard (1955) on *Cephalcia marginata*. Matsuda (1970) has also described an equivalent condition in *Pamphilius luteicornis* but with the difference that he has shown the presence of a narrow bridge which connects the protergum and the mesoepisternum. However, close observation reveals that this bridge is not a sclerotic connection but is a forward extension of the mesoepisternum and which is distally in membranous connection with the protergum.

Conditions are different in the rest of the higher symphytans. In *Pristiphora cincta* (Fig. 5), *Pachyprotasis brunetti* and *Tomostethus* (*Eutomostethus*) *assomensis* (Tenthredinidae) *Neodiprion abietis* (Fig. 3) (Diprionidae), *Arge clavicornis* (Fig. 4) (Argidae), *Cimbex americana americana* (Fig. 6) (Cimbridae), *Cephus* (*Cephus*) *cinctus* (Fig. 7) (Cepidae), *Xiphodria mellipes* (Fig. 8) (Xiphodridae) and *Sirex cyaneus* (Fig. 9) (Siricidae), the protergum is closely attached to the mesotergum and the membranous area between it and the mesoepisternum is reduced further.

The antero-lateral angles of the protergum are drawn out in the form of a triangular extension reaching far up to the base of the procoxa. As such it seems to be a part of the mesothorax girdling the latter anteriorly. An almost similar condition has also been shown by Snodgrass (1910) in *Arge* sp., *Tremex columba*, *Lygaenematus erichsonii*, Bird (1926) in *Hoplocampa halcyon*, Reeks (1937) in *Diprion polytomum*, Arora (1953) in *Diprion pini*, Bracken (1961) in *Anoplonyx luteipes*, Tait (1962) in *Perga affinis affinis*, Wong (1963) in *Pristiphora erichsonii* and Dhillon (1966) in *Athalia proxima*.

Members of the group Hymenoptera Parasitica show a further modification over the condition described up to this point. In *Sycoscapter stabilis* (Figs. 10, 11) (Torymidae-Chalcidoidea) the posterior margin of the protergum abuts against the mesotergum, thereby forging a tighter connection, and the membranous area between it and the episternum is further reduced. However, the ventral extensions of the antero-lateral angles of the pronotum are of the similar pattern as above. Similar observations have been made in the other chalcids studied including *Walkerella temeraria* and *Micranisa pteromaloides* (Torymidae), *Sycophila decatomoides* (Eurytomidae) and *Blastophaga masoni* (Agaonidae). Snodgrass (1910) has also shown a similar condition in the chalcids under his observation. In the members of the Superfamily Ichneomonoidea such as *Netelia kashmirensis* (Figs. 12, 13) and

Trachysphyrus sp. (Figs. 14, 15), further modifications to this effect are traceable. In them the ventral extension of the antero-lateral corners of the protergum is more pronounced. They reach far down on the sides, fitting into the space between the base of the procoxa and mesopleuron. Moreover the protergum is more firmly attached with the mesonotum than even in the case of the chalcids. Snodgrass (1910), Alam (1951) and Jonathan and Gupta (1973) have made similar observations.

In the male representatives of the families Formicidae (Figs. 24, 25 and 26 to 29) and Mutillidae, conditions are similar to those which prevail in ichneumonids but in the females of *Dorylus labiatus* (Fig. 34) (Formicidae) and *Mutilla* sp. (Fig. 35) (Mutillidae), conditions are further modified. The posterior and postero-lateral angles of the protergum have become completely fused with the corresponding anterior margin of the mesonotum, and this fusion is such that even the lines of fusion are not traceable. Studying only these insects, one can easily be misled to believe the protergum to be a part of the mesothorax. However, after comparing the female representatives with the males of these species, it becomes quite clear that in females the fusion of the protergum with the mesonotum is only a secondarily acquired character. The propectus lies much ahead and looks entirely disassociated from the protergum.

The second line of modification covers the rest of the families of suborder Apocrita. In *Chrysis indogotea* (Figs. 16, 17) (Chrysididae), *Scolia quadripustulata* (Figs. 18, 19) (Scoliidae), *Vespa orientalis* (Figs. 20, 21) (Vespidae), *Eumenes dimidiatepennis* (Figs. 22, 23) (Eumenidae), the conditions resemble very much those of the ichneumons. In them the postero-lateral angles of the protergum extend to cover the spiracles and these extensions can be compared with the spiracular lobe of the honeybee (Snodgrass, 1925). On the other hand, the antero-lateral angles of the protergum are almost equal to those seen in the ichneumons.

Conditions are further modified in the members of family Sphecidae. In *Scelephron intrudens* (Figs. 30, 31), *Stizus vespiformis* (Figs. 32, 33), the ventral extensions of the antero-lateral angles of the protergum are much more pronounced. These extensions, after flanking the sides, also extend on the ventral aspect of the prothorax so as to come close to one another along the mid-ventral line without actually fusing. Thus the entire pronotum appears to form a collar skirting the mesothorax along its anterior boundary. Prothoracic spiracles in these cases are completely covered over by the well developed spiracular lobes which extend laterally in the postero-lateral angles of the protergum. In the case of *Xylocopa lemuiscapa* (Figs. 36, 37), a member of superfamily Apoidea, ventral extension of the protergum, after flanking the sides of the segment, not only lie close to one another but they actually fuse to form a ventral plate between the prosternum and the mesosternum. In this way, the protergum forms an entire annulus which encircles

the mesothorax along its anterior margin. In this process it gets far removed from the propectus as well, with which it has only membranous connection. The propectus occurs in a much forward position with only its posterior tip lying just in the enclosure of the protergum. Similar conditions have also been noted in some other unidentified specimens of this superfamily. This observation is further substantiated by similar studies made by Snodgrass (1910) in honeybee and in *Proctotrypes candatus*. This stage probably represents the most advanced stage of evolution as far as the disassociation of protergum from the propectus and the complete transformation of the former from a dorsal plate into an annular sclerite are concerned. This evolutionary stage is also seen in the association of the pronotum with its lateral extensions covering the two first spiracles in the form of lobes.

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INSECTS ASSOCIATED WITH WEEDS IN THE NORTHEASTERN
UNITED STATES. II. CINQUEFOILS, *POTENTILLA*
NORVEGICA AND *P. RECTA* (ROSACEAE)¹

S. W. T. Batra

Abstract.—Eighty species of insects, including 15 crop pests and 8 pollinators, are associated with *Potentilla norvegica* L. and *P. recta* L. in the northeastern United States. Among the pests are the strawberry root weevil, *Otiorhynchus ovatus* (L.), and the strawberry aphid, *Chaetosiphon fragaefolii* (Cockerell). A biological control program using insects against these weeds would be difficult due to the close genetic relationship between strawberries and cinquefoils, and probable consequent attractiveness of *Fragaria* to phytophagous insects that attack *Potentilla*.

Introduction

A survey of phytophagous insects and pollinators of the rough cinquefoil, *Potentilla norvegica* L. and the sulfur cinquefoil, *P. recta* L., was undertaken to determine the trophic niches occupied by North American insects. According to Werner and Soule (1976), there is no readily available information regarding insects affecting cinquefoils.

The genus *Potentilla* consists of about 300 primarily Holarctic species with a wide range of polyploidy (Kohli and Denford 1977), of which there are over 50 species in North America, but only about five of these are weedy.

Potentilla norvegica (2N = 70) is an annual, biennial or perennial of Holarctic origin with two subspecies: *norvegica*, being native to northern Eurasia; and *monspeliensis* (L.) Asch. and Gr., which originates in North America (Hultén 1974). *Potentilla recta* (2N = 28, 42; Darlington and Wylie 1956) is a perennial of Eurasian origin that has become established primarily in northeastern North America (Frankton and Mulligan 1970). There are three North American varieties: *sulphurea* (Lam. and DC.) Peyr., *obscura* (Nestler) Koch., and *pilosa* (W.) Led. (Werner and Soule 1976). Both species spread by dispersal of achenes.

In the northeastern and north central United States, cinquefoils are among the most important weeds in forage crops, lawns, pastures and hay (Danielson et al. 1965). Although cinquefoils may be controlled by cultivation or

¹ This is the second publication in a series on native insects associated with introduced weeds in the northeastern United States. Other genera investigated are: I, *Galinsoga* (Environ. Entomol., in press); III, *Stellaria* (J. New York Entomol. Soc., in press); *Hieracium*, *Galium*, *Galeopsis*, *Lychnis* (= *Melandrium*), *Cerastium*, *Sonchus*, and *Matricaria* (in preparation).

application of herbicides such as 2, 4-D or Silvex (the mention of a pesticide in this paper does not constitute a recommendation of this product by the USDA) (Werner and Soule 1976), control of these weeds in strawberries is difficult (Anonymous 1976). Cinquefoils are closely related to strawberries and some species have recently been hybridized with them by breeders for strawberry improvement (Scott and Lawrence 1976; Barrientos-Perez 1976). Other beneficial uses of cinquefoils are as ornamentals, including a variety of *P. recta*, "Warrensii"; for tannins (Werner and Soule 1976); as forages (Chevtava 1975); and as a source of anti-bacterial chemicals (Makarenko and Chaika 1974).

Materials and Methods

Phytophagous insects and pollinators of *P. norvegica* and *P. recta* were collected in Virginia, Maryland, Pennsylvania, New Jersey and New York during three years (1975-1977), at 15 locations for each species. The insects were observed, then hand-picked, aspirated or netted from plants in the field, and any feeding damage was noted. These plants were cut or uprooted, placed in large plastic bags, removed in the laboratory, and examined and beaten against a white oilcloth to loosen clinging insects. The plants were then placed in large clean plastic bags with netting caps for development or emergence of additional insects. The bagged plants were kept in the laboratory for about a month or until they decomposed and insects ceased to emerge. Most surveyed cinquefoil was collected in vacant lots or weedy pastures with a mixed plant population, but some plants were in cultivated fields.

Results and Discussion

Phytophagous insects and pollinators associated with *P. norvegica* and *P. recta* are listed in Table 1. Some additional insects associated with the introduced species *P. intermedia* L. in New York are as follows: Pseudocidae, the lampyrid beetle *Pyropyga minuta* Le Compte, the weevils, *Anthonomus* sp. nr. *consimilis* Say and *Ceutorhynchus* sp., and the leafhopper *Graphocephala* sp. Unidentified tortricid, geometrid, and noctuid (Hermiinae) larvae were collected on the native *P. canadensis* L. in Maryland. Cinquefoils benefit from cross pollination to set the abundant seed necessary for their propagation, but some species, including *P. recta*, may reproduce agamosperously (Werner and Soule 1976). In a survey of insects visiting flowers of various weeds, Mulligan and Kevan (1973) found that flowers of *Potentilla* are unattractive. However, Mitchell (1960, 1962) lists 45 species of Apoidea in 21 genera as visiting cinquefoil flowers. Table 1 includes ants, bees and syrphid flies as pollinators. Cinquefoils are hosts of yellows viruses (Surgucheva 1976), that may be transmitted to crops by some of the Ho-

Table 1. Insects associated with cinquefoil. Relative frequency: C, commonly collected at most locations; M, moderate abundance, collected at 3–5 locations; R, rare, only 1 or 2 specimens, or found at less than 3 locations; —, not collected. Plant parts affected: F, flower, L, leaf, S, stem, Rt, root. Remarks: P, pollen feeder; N, nectar feeder; V, probable vector to crops of yellows virus occurring in *Potentilla*; numbers refer to months when insects were collected.

	Relative frequency		Plant part affected	Remarks
	<i>P. norvegica</i>	<i>P. recta</i>		
COLEOPTERA				
Bruchidae				
<i>Bruchus brachialis</i> F.	R	—	F	8, Pest
Cantharidae				
<i>Chauliognathus</i> sp.	—	M	L, S	7
Chrysomelidae				
Alticine larvae	R	—	L	8
Chrysomelid larvae	R	—	L, S	7
<i>Longitarsus</i> sp.	—	R	L, S	7
<i>Sumitrosis ancoroides</i>	—	R	L, S	7
Curculionidae				
<i>Calomycterus setarius</i> Roelofs	—	R	Rt	7, introduced
<i>Gymnetron pascuorum</i> (Gyllenhal)	—	R	L, S	7
<i>Hypera nigrirostris</i> (F.)	—	R	L, S	7
<i>Oedophyrus hilleri</i> (Faust)	C	—	L, S	7, 8, introduced
<i>Otiorhynchus ovatus</i> (L.)	R	—	Rt	11, Pest
<i>Tychius picrostris</i> (F.)	C	—	L, S	7, 9, Pest
Nitidulidae				
<i>Brachypterolus pulicarius</i> L.	—	R	F	6, introduced also on strawberry
<i>Meligethes nigrescens</i> Stephen	R	—	F	7, Pest
Scarabaeidae				
<i>Popillia japonica</i> Newman	C	—	L	7, Pest, introduced
DIPTERA				
Cecidomyiidae				
<i>Mycodiplosis inimica</i> (Fitch)	—	C	L, S, F	8, feeds on rust spores
<i>Mycodiplosis thoracica</i> (Fitch)	—	C	L, S, F	8, feeds on rust spores
Syrphidae				
<i>Sphaerophoria contigua</i> (Macquart)	—	M	F	6, N, also predaceous larvae
<i>Sphaerophoria philanthus</i> (Meigen)	—	R	F	6, N, also predaceous larvae
<i>Toxomerus geminatus</i> (Say)	—	C	F	6, 8, N, also predaceous larvae

Table 1. Continued.

	Relative frequency		Plant part affected	Remarks
	<i>P. norvegica</i>	<i>P. recta</i>		
<i>Toxomerus marginatus</i> (Say)	—	C	F	6, 7, N, also predaceous larvae
HEMIPTERA				
Berytidae				
<i>Jalysus spinosus</i> (Say) nymphs	—	M	L, F	6, Pest
Miridae				
<i>Lygus lineolaris</i> (Palisot de Beauvois)	C	C	F	7, Pest
<i>Psallus</i> sp.	—	R	F	8
Tingidae				
<i>Corythucha marmorata</i> (Uhler)	—	R	L, S	6
HOMOPTERA				
Aleyrodidae				
Aleurodicine sp.	R	—	L	9
Aphididae				
<i>Acyrtosiphon</i> sp.	R	C	L, S	6, 7
Aphid spp. nymphs	R	C	L, S	6
<i>Aphis</i> sp.	—	R	L, S	7, 8
<i>Chaetosiphon fragaefolii</i> (Cockerell)	C	—	L, S	7, 8, Pest
<i>Macrosiphina</i> sp.	—	C	L, S	6, 8
<i>Macrosiphum euphorbiae</i> (Thomas)	C	C	L, S	6, 7, 11, Pest
<i>Myzus persicae</i> (Sulzer)	M	—	L, S	11, V, Pest
<i>Rhopalosiphum maidis</i> (Fitch)	C	—	L, S	8, 11, Pest
<i>Schizaphis graminum</i> (Rondani)	R	—	L, S	11, Pest
Cercopidae				
Cercopid nymphs	M	—	L, S	6
<i>Philaenus spumarius</i> (L.)	—	C	L, S	6, V, Pest
Cicadellidae				
<i>Agallia constricta</i> Van Duzee	M	R	L, S	6
<i>Aphrodes bicinctus</i> (Schrank)	—	M	L, S	7
Cicadellid nymphs	M	—	L, S	7, 8
Deltocephaline nymphs	M	—	L, S	8
<i>Graphocephala versuta</i> (Say)	C	—	L, S	7, 8
<i>Gyponana</i> sp. nymphs	M	—	L, S	6
<i>Macrosteles fascifrons</i> (Stål)	R	—	L, S	9, V, Pest
Flatidae				
<i>Anormenis</i> sp. nymphs	—	R	L	7
Membracidae				
Membracid nymphs	—	M	L, S	6
Pseudococcidae				
Pseudococcid nymphs	M	C	Rt	7, 8

Table 1. Continued.

	Relative frequency		Plant part affected	Remarks
	<i>P. norvegica</i>	<i>P. recta</i>		
HYMENOPTERA				
Apidae				
<i>Apis mellifera</i> L.	M	—	F	8, N
Formicidae				
<i>Lasius neoniger</i> Emery	—	C	F	7, N
<i>Leptothorax</i> sp.	—	R	F	6, N
<i>Monomorium minimum</i> (Buckley)	C	C	F	6, N
Halictidae				
<i>Dialictus mitatus</i> (Smith)	M	M	F	8, N, P
<i>Dialictus uncinus</i> (Sandhouse)	—	M	F	7, N
<i>Halictus confusus</i> Smith	R	—	F	8, N
<i>Halictus ligatus</i> Smith	R	R	F	6, 8, N
Tenthredinidae				
Fenusini larvae	R	—	L	7
LEPIDOPTERA				
Blastobasidae				
Blastobasid sp.	—	R	Rt	6
Geometridae				
<i>Eupathecia</i> sp. larvae	R	—	L, S	7, 8
Geometrid larvae	—	R	L, S	7
Lycaenidae				
<i>Lycaena</i> sp. larvae	R	—	L, S	7
Microlepidoptera sp.	R	—	Rt	8
Noctuidae				
<i>Lacinipolia</i> sp. larvae	—	R	Rt	7
Noctuid larvae	M	M	L, S	6
<i>Plathypena scabra</i> (Fabricius) larvae	R	—	L, S	7
Plusiine larvae	R	—	L, S	8
<i>Pyrhia umbria</i> (Hufnagel) larvae	—	M	L, S	8
Pyralidae				
<i>Pyrausta</i> sp. larvae	R	—	L, S	11
Tortricidae				
<i>Platynota</i> sp. larvae	M	R	L, S	6, 8
<i>Sparganothis sulphurana</i> (F.) larvae, adults	M	C	L, S	6, 7
Tortricid larvae	M	—	L, S	11
ORTHOPTERA				
Gryllidae				
<i>Oecanthus</i> sp. nymphs	—	R	L	6
PSOCOPTERA				
Ectopsocidae				
<i>Ectopsocopsis cryptomeriae</i> (Enderlin)	—	R	L	7

Table 1. Continued.

	Relative frequency		Plant part affected	Remarks
	<i>P. norvegica</i>	<i>P. recta</i>		
THYSANOPTERA				
Idolothripinae				
Apterous	—	R	L, F	7
Winged form	—	R	L, F	6
Thripidae				
<i>Frankliniella fusca</i> (Hinds)	C	C	L, F	6, 7, 8, Pest
<i>Frankliniella tritici</i> (Fitch)	C	C	L, F	6, 7, 8, Pest
<i>Sericothrips variabilis</i> (Beach)	R	—	L	11
<i>Taeniothrips atratus</i> (Haliday)	R	—	L, F	8
Thripidae sp.	R	—	L, F	7
<i>Thrips tabaci</i> Lindeman	C	—	L, F	6, Pest

moptera listed in Table 1. They were also hosts of 15 crop pests, including two species that attack strawberries. These weeds were not severely damaged by the insects listed here. Cinquefoils were frequently attacked and damaged by rust fungi, which were eaten by cecidomyiid larvae.

Due to the close genetic and physiological similarity between cinquefoils and strawberries, it may be difficult to locate specific biological control agents that will not also attack *Fragaria*. The initiation of a biological control program for these weeds is therefore not highly recommended.

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INSECTS ASSOCIATED WITH WEEDS IN THE NORTHEASTERN
UNITED STATES. III. CHICKWEED, *STELLARIA MEDIA*, AND
STITCHWORT, *S. GRAMINEA* (CARYOPHYLLACEAE)

S. W. T. Batra

Abstract.—156 species of phytophagous and pollinating insects and 3 phytophagous mites are associated with the introduced Eurasian chickweeds, *Stellaria media* L. (Cyrillo) and *S. graminea* L. in the northeastern United States. Among these are 16 crop pests, including three known vectors of crop viruses that also infect *S. media*. Pollinators are primarily Apoidea, Syrphidae and Formicidae. The collection of *Tmetothrips subapterus* (Haliday) on *S. graminea* represents the first Western Hemisphere record. *Stellaria media* ranks among the ten most important weeds in the United States. A biological control program is possible, although it may be difficult due to the habit and habitat of this winter annual.

A survey of phytophagous insects of the introduced common chickweed, *Stellaria media* (L.) Cyrillo, and stitchwort or little starwort, *S. graminea* L. was undertaken to determine the trophic niches occupied by North American insects before initiating foreign exploration for possible biological control agents.

Stellaria media is a weed associated with people in Europe since prehistoric times (King 1966). It is now ubiquitous (Coquillat 1951), occurring in moist, fertile, disturbed soils throughout much of the world including the tropics (Hultén 1970), where it may occur as a winter annual during the cool season or at high elevations (Chopra et al. 1956; Cardenas et al. 1970). Chickweed is a very variable, polymorphic species ($2n = 28, 40, 42, 44$; Darlington and Wylie 1956; Blackburn and Morton 1957) with several ecotypes (King 1966), subspecies and varieties (Hultén 1970). In the temperate zones it is a winter annual or biennial. The plants germinate in late summer, grow during fall, and remain green throughout winter, while surviving -12°C temperature (due to high cell sugar content), and producing fertile seeds in the cleistogamous flowers (King 1966). Rapid growth and open pollination begin in early spring; most plants die before midsummer. The winter growth of *S. media* resembles that of arctic *Stellaria* spp. (Bell and Bliss 1977). This suggests that chickweed may be a post-glacial relict, perhaps originally occurring on nutrient-rich moraine deposits, later becoming associated with human refuse dumps, and as agriculture developed, invading fertile fields. Chickweed requires neutral soil pH (Buchanan et al. 1975), a high nitrogen level (King 1966), and is sensitive to phosphorous deficiency (Hoveland et

al. 1976). The small seeds are transported by ants (King 1966). They can remain viable while buried under 27.0 or 7.5 cm of soil for 32 or 58 years, respectively (Harper 1960). Optimal seed depth for germination is 0.5 to 1 cm; maximum is 2 cm; alternating temperature (20–30°C) is beneficial (Andersen 1968; Thompson et al. 1977). Viable seeds in soil may reach densities of 12.5 million per hectare (4 Kg.) in pastures, and 24.6 million per hectare in arable areas (King 1966); chickweed seed is also abundant in marshland soils (Hunyadi and Pathy 1976). Individual plants may produce 2,200–2,700 seeds (Kavanagh 1974). Although Mulligan and Kevan (1973) found no insects visiting the small, white autogamous flowers of *S. media*, Mitchell (1962, 1966) lists 34 bee species in 10 genera on *Stellaria*. Philipp (1975) found that seed setting in the self-fertile, arctic *S. longipes* Goldie was enhanced by frequent visits by insects; the alpine species, *S. cerastioides* L., is pollinated by empid, muscid and syrphid flies (Müller 1881). *Stellaria media* flowers in early spring are an important food source for many bees, wasps and flies (Table 1); *S. graminea* flowers in summer also attract many insects (Table 1; Müller 1881).

Common chickweed ranks among the ten most important weeds in the United States (Jansen et al. 1972), where it is widespread (Fernald 1970). It is a major pest in wheat, small grains, legume seed crops, and potatoes; in vegetables such as asparagus, legumes, root crops, greens, salad crops and cole crops; also in stone fruits, ornamentals, lawns, turf, hay and pastures (Vengris 1953; Jansen et al. 1972). Chickweed invades 26 crops in 40 states, particularly in the northeast and south; and it occupies over 2.8 million acres of cultivated cropland (Jansen et al. 1972). The rapidly growing plants in early spring effectively compete with crop seedlings for nutrients, water and light (Welbank 1963; Gibson and Courtney 1977); however, chickweed may be used to suppress the growth of bindweeds in vineyards (Stalder et al. 1977). In Europe it invades overgrazed pasture (Haggard 1974), dominates recently uncultivated land (Covarelli 1976), and is abundant in crops such as winter and spring cereals, barley, wheat, oats, pulses, linseed and carrots (Granström and Almgard 1955). Common chickweed in row crops is controlled by various herbicides (Aldrich 1957; Gummeson 1976; Parochetti and Bell 1975).

Stellaria graminea, a perennial and also native to Eurasia, occurs in grasslands in north central and northeastern North America (Fernald 1970). In Quebec it occurs in cultivated fields, but it is more abundant in cereals, young and old meadows (Hamel and Dansereau 1949). In eastern Europe it is common in prairie (Hruska-Dell'Uomo 1976) and floodplain meadows (Shcherbach 1977). There are three European cytotypes: diploids ($2N = 26$); triploids ($2N = 39$) and tetraploids ($2N = 52$; Gadella 1977). The triploid plants are male-sterile and do not produce viable seed; although not previously reported outside the Netherlands (Gadella 1977), I often found

Table 1. Insects and mites associated with *Stellaria*. Relative frequency: C, commonly collected at most locations; M, moderate abundance, collected at 3–5 locations; R, rare, only 1 or 2 specimens or found at less than 3 locations; —, not collected. Plant parts affected: F, flower; L, leaf; S, stem; Rt, root. Remarks: P, pollen feeder; N, nectar feeder; V, vector of crop viruses. Numbers refer to months of collection.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
ACARINA				
Tetranychidae				
<i>Bryobia praetiosa</i> Koch	C	—	L, S	4, 5, 10
<i>Tetranychus</i> sp. immatures	R	—	L, S	11
<i>Tetranychus urticae</i> Koch	R	—	L, S	11, Pest
COLEOPTERA				
Cantharidae				
<i>Cantharis</i> sp.	R	—	L, S	5
Chrysomelidae				
<i>Disonycha</i> sp. larvae	C	—	L, S	6, defoliates
<i>Oedionychis</i> sp. larvae	—	M	L, S	7
<i>Phyllotreta sinuata</i> (Stephens)	R	—	L, S	6
Curculionidae				
<i>Hypera</i> sp. larvae	—	M	S	7
<i>Idiostethus</i> sp.	—	R	S	7
<i>Odontocorynus scutellum-album</i> (Say)	—	M	F	6, P
Dermestidae				
<i>Anthrenus scrophulariae</i> (L.)	—	R	F	7, P
Elateridae				
<i>Conoderus bellus</i> (Say)	R	—	Rt	5
Nitidulidae				
<i>Glischrochilus quadrisignatus</i> (Say)	R	—	F	5
<i>Meligethes nigrescens</i> (Stephens)	M	—	F	5, Pest
COLLEMBOLA				
Entomobryidae				
<i>Lepidocyrtus alleghanyensis</i> Maynard	M	—	S, Rt	4
Isotomidae				
<i>Isotoma viridis</i> Bourlet	R	—	S, Rt	4
<i>Proisotoma minuta</i> Tullberg	R	—	S, Rt	4
Poduridae				
<i>Xenylla grisea</i> Axelson	M	—	S, Rt	4
DIPTERA				
Acalyptratae				
<i>Acalyptrate</i> sp.	—	R	L, S	7

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
Agromyzidae				
Agromyzid larva	R	—	L	7
<i>Melanagromyza buccalis</i> Spencer	—	R	F	7
Anthomyiidae				
<i>Hylemya platyura</i> (Meigen)	M	—	F	3, 4, N
<i>Pegomya</i> sp. larvae	R	—	L, S	10
Anthomyzidae				
<i>Anthomyza</i> sp.	R	—	F	6
<i>Munetopia occipitalis</i> Melsheimer	C	—	F	4, 6, N
Calliphoridae				
<i>Phormia regina</i> (Meigen)	R	—	F	4, N
Chloropidae				
<i>Elachiptera erythropleura</i> Sabrosky	M	—	S, Rt	6
<i>Elachiptera nigriceps</i> (Loew)	R	—	S, Rt	6
<i>Hippelates dissidens</i> (Tucker)	M	—	S, Rt	4
<i>Monochaetoscinella nigricornis</i> (Loew)	R	—	S	6
<i>Olcella trigramma</i> (Loew)	C	—	S, Rt	6
<i>Oscinella carbonaria</i> (Loew)	C	—	S, Rt	4, 6, Pest
<i>Oscinella melancholica</i> Beck	M	—	S, Rt	6
<i>Oscinella soror</i> (Macquart)	C	R	S, Rt	6, Pest
<i>Oscinella umbrosa</i> (Loew)	R	—	S, Rt	6
Drosophilidae				
<i>Drosophila busckii</i> (Coquillett)	R	—	S, Rt	10
Orthocladine larvae	C	—	S, Rt	6
<i>Scaptomyza adusta</i> (Loew)	M	—	S, Rt	3, 4, 6, 10
<i>Scaptomyza pallida</i> (Zetterstedt)	C	—	S, Rt	3, 4, 6, 10
Otitidae				
Otitid larvae	M	—	S	6

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
Stratiomyidae				
Stratiomyid larvae	M	—	S	6
Syrphidae				
<i>Carposcalis obscurum</i> (Say)	C	—	F	4, N
<i>Eristalis arbustorum</i> (L.)	—	R	F	6, N
<i>Eristalis dimidiatus</i> Wiedemann	—	C	F	6, N
<i>Eristalis tenax</i> (L.)	—	R	F	6, N
<i>Helophilus fasciatus</i> Walker	—	R	F	6, N
<i>Helophilus latifrons</i> Loew	—	R	F	6, N
<i>Megasyrphus latus</i> (Osten Sacken)	—	M	F	6, N
<i>Metasyrphus americanus</i> (Weidemann)	R	—	F	3, N
<i>Metasyrphus lapponicus</i> (Zetterstedt)	—	M	F	6, N
<i>Parhelophilus laetus</i> (Loew)	—	R	F	6, N
<i>Platycheirus quadratus</i> Say	R	—	F	3, N
<i>Sphaerophoria contigua</i> (Macquart)	C	—	F	11, N
<i>Sphaerophoria philanthus</i> Meigen	R	C	F	4, 6, N
<i>Syritta pipiens</i> (L.)	—	M	F	6, N
<i>Syrphus rectus</i> Osten Sacken	—	M	F	6, N
<i>Syrphus torvus</i> Osten Sacken	—	M	F	6, N
<i>Syrphus vitripennis</i> Meigen	—	R	F	6, N
<i>Toxomerus geminatus</i> (Say)	—	R	F	6, N
<i>Toxomerus marginatus</i> (Say)	C	R	F	4, 6, N
<i>Xylota hinei</i> (Curran)	—	R	F	6, N
Tachinidae				
<i>Epalpus signifer</i> (Walker)	M	—	F	3
<i>Gonia</i> sp.	R	—	F	4
<i>Gymnocyttia occidua</i> (Walker)	—	R	F	6

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
HEMIPTERA				
<i>Lygus lineolaris</i> (Palisot de Beauvois)	—	R	L, S, F	6
Mirid nymphs	C	R	L, S, F	6, 7, damage meristem
Pentatomidae				
<i>Cosmopepla bimaculata</i> (Thomas)	—	R	F	6
Pentatomid nymphs	C	R	L, S	7
HOMOPTERA				
Aphididae				
<i>Acyrtosiphon</i> sp.	—	R	L, S	6, 7
<i>Acyrtosiphum sibericum</i> (Mordv.)	M	—	L, S	4, 6
<i>Aphidius</i> sp.	C	—	L, S	4, 6
Aphidini nymphs	M	M	L, S	6
<i>Aphis</i> sp.	C	—	L, S	2
<i>Aphis gossypii</i> (Glover)	R	—	L, S	9, Pest
<i>Dactynotus</i> sp.	—	R	L, S	7
<i>Hyalopterus pruni</i> (Geoffroy)	R	—	L, S	4
Macrosiphini nymphs	M	R	L, S	6, 11
<i>Macrosiphum euphorbiae</i> (Thomas)	C	—	L, S	4, 6, 9, Pest
<i>Myzus</i> sp.	M	—	L, S	5
<i>Myzus persicae</i> (Sulzer)	C	—	L, S	2, 4, 5, 6, 7, 9, 10, 11, V, Pest
<i>Rhopalosiphum maidis</i> (Fitch)	R	—	L, S	11, Pest
<i>Rhopalosiphum padi</i> (L.)	C	—	L, S	10, 11
<i>Schizaphis graminum</i> (Rondani)	C	—	L, S	10, 11
Cercopidae				
Cercopid nymph	R	R	L, S	4, 9
<i>Philaenus spumarius</i> (L.)	R	C	S	6, Pest
Cicadellidae				
<i>Agallia</i> sp.	M	—	L, S	6
<i>Agallia constricta</i> (Provancher)	M	—	L, S	2, 4
<i>Aceratogallia sanguinelenta</i> Van Duzee	M	—	L, S	9
Cicadellid sp. nymphs	C	R	L, S	6, 7, 9, 11
Deltocephaline nymphs	M	—	L, S	7

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
<i>Doratura stylata</i> (Boh.)	—	M	L, S	7
<i>Empoasca</i> sp.	R	M	L, S	9
<i>Empoasca erigeron</i> DeLong	R	—	L, S	6
Gyponine nymphs	R	—	L, S	6
HYMENOPTERA				
Andrenidae				
<i>Andrena</i> spp.	M	M	F	3, 4, 5, 6, 7, N
<i>Andrena carlini</i> Cockerell	C	—	F	4, N, P
<i>Andrena dunningi</i> Cockerell	—	R	F	6, N, P
<i>Andrena signuandi</i> Cockerell	R	—	F	4, N, P
<i>Andrena viburnella</i> Graenicher	R	—	F	4, N
<i>Andrena vicina</i> Smith	C	—	F	4, N
<i>Calliopsis andreni-</i> <i>formis</i> Smith	—	M	F	7, N, P
Anthophoridae				
<i>Xylocopa virginica</i> (L.)	M	—	F	3, N
Apidae				
<i>Apis mellifera</i> L.	M	—	F	4, N, P
<i>Bombus bimaculatus</i> Cresson	R	—	F	3, N
<i>Bombus ternarius</i> Say	—	M	F	7, N
<i>Bombus terricola</i> Kirby	—	M	F	7, N
Braconidae				
<i>Chelonus</i> sp.	—	R	F	6, N
Formicidae				
<i>Camponotus novebor-</i> <i>censis</i> (Fitch)	—	R	F	6, N
<i>Formica subsericea</i> Say	—	R	F	6, N
<i>Leptothorax muscorum</i> (Nylander)	—	M	F	7, N
<i>Myrmica lobicornis</i> <i>fratricornis</i> Emery	—	R	F	6, N
<i>Prenolepis imparis</i> (Say)	M	—	F	4, N
<i>Tapinoma sessile</i> (Say)	M	M	F	6, 7, N
Halictidae				
<i>Dialictus lineatulus</i> (Crawford)	—	M	F	7, N
<i>Dialictus versatus</i> (Robertson)	R	M	F	4, N

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
<i>Halictus confusus</i> Smith	—	C	F	7, N
<i>Halictus rubicundus</i> (Christ)	—	R	F	7, N
<i>Lasioglossum forbesii</i> (Robertson)	—	R	F	7, N, P
Ichneumonidae				
<i>Banchus flavescens</i> Cresson	—	R	F	6, N
<i>Exyston chlavatum</i> (Cresson)	—	R	F	6, N
Megachilidae				
<i>Osmia cornifrons</i> (Radoszkowskii)	M	—	F	4, N, introduced
Pompilidae				
<i>Anoplius</i> sp.	—	M	F	6, 7, N
Vespidae				
<i>Polistes fuscatus</i> (F.)	R	—	F	3, N
LEPIDOPTERA				
Arctiidae				
<i>Diacrisia</i> sp. larvae	M	—	L, S	9
Coleophoridae				
<i>Coleophora</i> sp. larvae	—	R	L, S	6
Gelechiidae				
<i>Stomopteryx</i> sp.	R	—	Rt	4
Geometridae				
<i>Eupathecia</i> larvae	R	—	L, S	6
Geometrid larvae	R	—	L, S	9
Microlepidoptera adult	—	R	S	7
Noctuidae				
<i>Amphipyra pyramidoides</i> Guenée	R	—	L	5
<i>Amathes badinodis</i> (Grote)	R	—	L, S	4
<i>Eupsilia</i> sp. larvae	R	—	L, S	4
<i>Euxoa</i> sp. larvae	R	—	L, S	5
<i>Lacinipolia</i> sp. larvae	R	—	L, S	4
Noctuid larvae (1st instar)	C	—	L, S	4, 5
<i>Plathypena scabra</i> (F.) larvae	M	—	L, S	9
Plusiine larvae (1st instar)	R	—	L, S	4

Table 1. Continued.

	Relative frequency on		Plant part affected	Remarks
	<i>S. media</i>	<i>S. graminea</i>		
<i>Pseudaplusia</i> sp. larvae	R	—	L, S	10
Pyrilidae				
<i>Udea rubigalis</i> (Guenée) larvae	M	—	L, S	6, 9, Pest
Tortricidae				
<i>Sparganothis reticulana</i> (Clemens)	R	—	L, S	9
<i>Sparganothis sulphurana</i> (F)	R	R	L, S	7
Tortricid larvae	—	R	L	6
ORTHOPTERA				
Gryllidae				
<i>Anaxipha</i> nymph	R	—	L	4
THYSANOPTERA				
Phlaeothripidae				
<i>Haplothrips leucanthemi</i> (Schränk)	M	—	F	5, Pest
Thripidae				
<i>Anaphothrips obscurus</i> (Mueller)	M	—	L, S	4, 5, 6
<i>Aptinothrips rufus</i> (Mueller)	M	—	L, S	6
<i>Aptinothrips stylifer</i> Trybom	—	R	L, S	6, Pest
<i>Chirothrips</i> sp.	—	R	L, S	6
<i>Frankliniella fusca</i> (Hinds)	C	—	L, S	4, 6, 9, 10, 11 V, Pest
<i>Frankliniella tenuicornis</i> (Uzel)	R	—	L, S	10, V, Pest
<i>Frankliniella tritici</i> (Fitch)	M	M	L, S	6, Pest
<i>Limothrips cerealium</i> (Haliday)	R	—	L, S	5
<i>Taeniothrips atratus</i> (Haliday)	M	—	L, S	6
<i>Thrips physapus</i> L.	R	—	L, S	6
<i>Thrips tabaci</i> Lindeman	M	—	L, S	4, 10, Pest
<i>Tnetothrips subapterus</i> (Haliday)	—	C	L, S	6, European species, new record for New World

male-sterile plants (perhaps triploids) growing among normal plants at Trudeau, N.Y. Light or temperature (10 to 30°C) alternation benefits germination (Andersen 1968). This species, although common in meadows in upstate New York and New England, is much less weedy and invasive than *S. media*.

Materials and Methods

Phytophagous insects, mites and pollinators of *S. media* and *S. graminea* were collected at 41 and 13 locations, respectively, in Maryland, Pennsylvania, New York and Vermont during four years (1975–1978). The insects were observed, then they were hand-picked, aspirated or netted from the plants in the field, and any feeding damage was noted. The plants were then cut or uprooted, placed in large plastic bags, removed from the bags in the laboratory, examined, and beaten against a white oilcloth to loosen clinging insects. The plants were then placed in large, clean, clear plastic bags with netting caps for development and emergence of additional insects. The bagged plants were kept in the laboratory for about a month or until they decomposed and insects ceased to emerge. *Stellaria media* was collected from pastures, lawns, dumps, fallow land, forest edges, roadsides, and at edges of fields planted to soybeans, tomatoes and alfalfa. *Stellaria graminea* was collected from pastures, meadows, hayfields and roadsides.

Results and Discussion

Phytophagous insects and mites, and pollinators associated with chickweed and stichwort are listed in Table 1. Relatively few insects were common to both species of *Stellaria*; this may be largely due to differences in plant habitat and seasonal occurrence, since most *S. media* was collected in spring to early summer in southern Maryland, and most *S. graminea* was collected in mid- to late summer in northern New York.

Stellaria media is an important reservoir of crop viruses, such as beet curly top, tomato spotted wilt (Miller et al. 1960), turnip mosaic (Citir and Varney 1974), beet mild yellows (Hartleb and Bauer 1977), nepoviruses (Hanada and Harrison 1977), carnation ringspot (Rudel et al. 1977), cucumber mosaic (Bruckart and Lorbeer 1976; Kazda and Hervert 1977) and others (Kavanagh 1974). It is probable that viruses and other pathogens overwinter in this plant, and in its seeds, to be transmitted to crops in the spring (Kavanagh 1974). Insects that are known to transmit these crop viruses (Carter 1962), and that were collected on *Stellaria* are indicated in Table 1. Included in Table 1 are 16 species of crop pests harbored by *S. media* and *S. graminea* and 57 pollinators, belonging primarily to the Apoidea, Syrphidae and Formicidae. *Tmetothrips subapterus* (Haliday), collected on *S. graminea* at Rew, Pennsylvania, represents the first record of this

European monotypic genus in the Western Hemisphere. It lives in *Stellaria* galls and may be worthy of further investigation as a biological control agent (K. O'Neill, pers. comm.).

Stellaria media is eaten to some extent by 35 species of North American wildlife (mainly birds, Martin et al. 1951), and it is palatable to livestock, with good caloric content in winter (Caspers 1977). However, in view of its importance as a major weed, its lack of close relationship to valuable plants, its exotic origin and consequent lack of stenophagy or dependence by North American wildlife, it may be worthwhile to begin a search for potential biological control agents in Eurasia. However, its winter annual growth habit and usual predominance in cultivated areas do not favor the application of biological control methods. Insects and pathogens that destroy the flowers and seeds of chickweed would probably be the most effective control agents.

Except for numerous *Dysonychia* sp. larvae that totally defoliated plants at one Beltsville location, and mirid nymphs that damaged the meristem (Table 1) native North American insects did not appreciably affect *S. media*, as was expected. This weed seems to be an important overwintering reservoir or winter food source for crop viruses and insect pests such as *Myzus persicae* (Sulzer). The flowers provide food for beneficial insects such as bees and syrphid flies during late fall and early spring when few other flowers are blooming.

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THE LIFE HISTORIES OF THE *AUTODICE* AND *STERODICE*
SPECIES-GROUPS OF *TATOCHILA*
(LEPIDOPTERA: PIERIDAE)

Arthur M. Shapiro

Abstract.—The egg, larva, pupa and host relations of *Tatochila autodice*, *blanchardii*, *sterodice macrodice*, *sterodice sterodice*, *vanvolxemii* and *mercedis* are described. These species occur in temperate to subantarctic Argentina and Chile. The *sterodice* species-group is very homogeneous and seems to be closely related to *T. xanthodice* from Colombia. The *autodice* group shows many divergences in the larva and pupa and is convergent in various characters with a number of Holarctic taxa. *T. mercedis* is somewhat intermediate to the *autodice* group in certain characters.

This is the third in a series of papers describing the preparatory stages of the Pierini of the Andean region. This tribe has undergone an extraordinary adaptive radiation, with eight endemic genera and about 40 species in non-tropical habitats, from northeastern Colombia to Tierra del Fuego.

The biology of the genus *Tatochila*, *sens. lat.*, was reviewed by Giacomelli (1915) and Jörgensen (1916). The former prepared a hypothetical phylogenetic "tree" based on adult characters, mostly superficial. At that time the early stages of only one species, *T. autodice* (Hbn.) had been described, and even these had not been illustrated. When the genus was revised by Herrera and Field (1959) little more was known of its biology. *T. blanchardii* Butl. and *T. mercedis* (Esch.), common Chilean species, were reared but not published; *T. sterodice arctodice* Stgr. was studied as a truck-garden pest in an unpublished Colombian dissertation (Alvarez and Delgado 1969; Bravo *pers. comm.*). *T. autodice* has been redescribed several times, always unfigured, most recently by Margheritis and Rizzo (1965).

Recent studies (Shapiro 1978a, b and unpublished) indicate that the Andean Pierines are an important group for interpreting the historical biogeography and evolution of the regional biota. It thus becomes imperative to augment our knowledge of their biology. The descriptions which follow are based on field work in northern and central Argentina in 1977 and in southern Argentina in 1979 by the author, and in Chile in 1978 by Mr. C. V. Kellner. Alcoholic material will be deposited in the U.S. National Museum, Washington, D.C. and the University of California, Davis collections. Rearing was on continuous illumination at 25°C. Color descriptions in parentheses refer to the system of Kornerup and Wanscher (1978).

The *T. autodice* Species-Group

As defined by Herrera and Field this group contains two species and one subspecies. The adult characters make it a natural and very distinct group within the genus. Both species occur at low to moderate elevations.

Tatochila autodice (Hübner) (Fig. 1)

This is the common vacant-lot *mariposa blanca* of low elevations in northern and central Argentina. It colonizes in summer above 2000 m but does not seem to overwinter there. It is an occasional truck-garden pest, the *gusano rayado de las crucíferas* of Margheritis and Rizzo (1965). It was studied afield in the provinces of Tucumán, Córdoba, La Rioja, and Buenos Aires and in the Capital Federal (city of Buenos Aires) (26°49'S to 38°44'S). No geographic differences in morphology or development were observed.

Ecologically, *T. autodice* is largely confined to highly disturbed situations within regions supporting desert, subtropical forest, and temperate subhumid to subarid grassland biomes from at least 17°S to 40°S. Its occurrence in the desert is limited to river bottoms and washes. It is only an occasional stray in the humid Andes in Río Negro and Neuquén and does not normally breed at Bariloche. It is multivoltine throughout its range, with 5–6 broods in the northwestern provinces, about 4 at Buenos Aires, and perhaps 3–4 at Bahía Blanca. Winter is spent as a diapausing pupa. Diapause induction is under photoperiod-temperature control.

Eggs or larvae have been collected from the following wild crucifers in various locations: *Rapistrum rugosum* (L.), *Coronopus didymus* (L.) Smith, *Cardaria draba* (L.) Desv., *Cardamine hirsuta* L., *Diplotaxis muralis* (L.) DC., *Raphanus sativus* L., *Brassica geniculata* (Desf.) Ball (the most important host in Córdoba), *B. campestris* L., *B. napus* L., *Sisymbrium officinale* (L.) Scop., *S. irio* L., *Eruca sativa* Hill, *Conringia orientalis* (L.) Dumort, and *Nasturtium officinale* R. Br. (all introduced from the Palaearctic Region); and *Lepidium spicatum* Desv., *L. bonariense* L., *L. aletes* Macb., *Descurainia appendiculata* (Griseb.) Schulz and *D. argentina* Schulz (all native but weedy). Giacomelli (1915), citing Berg and Burmeister, recorded *T. autodice* on the genera *Cestrum* (Solanaceae) and *Medicago* (Leguminosae). Neither has been confirmed, and captive larvae rejected *Medicago sativa* L. and *M. hispida* Gaertn. Adults are common in alfalfa fields and often visit the flowers in the company of the alfalfa pest *Colias lesbia* (F.) and of *Tatochila vanvolxemii* (Capr.). Captive larvae do accept garden nasturtium, *Tropaeolum majus* L., and almost certainly use this indigenous genus (Tropaeolaceae) afield.

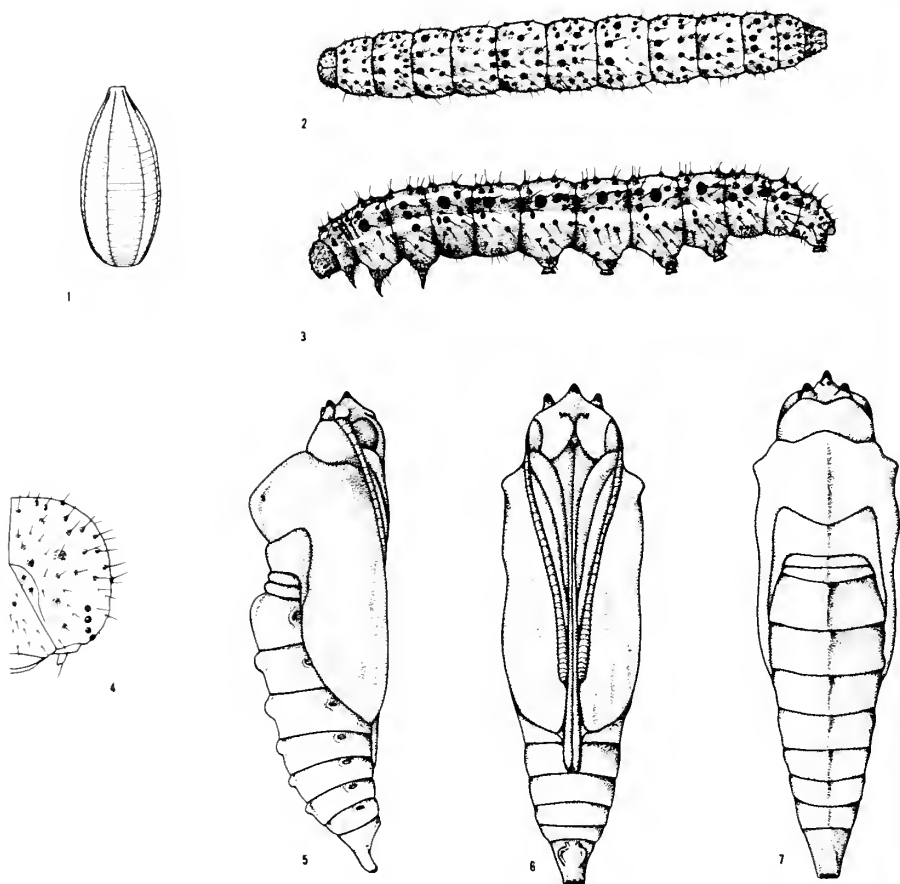


Fig. 1. *Tatochila autodice* from central Argentina: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, mature larva, head capsule; 5, pupa, lateral view; 6, pupa, ventral view; 7, pupa, dorsal view.

Descriptions

Egg.—Erect, milk-bottle shaped, 1.20×0.35 mm, the chorion sculptured as figured, with 8–10 vertical and about 32 horizontal ribs. Laid singly on leaves, stems, or inflorescences; when on leaves about equally on upper or lower surface. Often laid on small rosettes or on isolated plants along walls, hedgerows, or roadsides. Light orange when laid, darkening to deep orange after 12–18 h, translucent blackish 12 h before hatching. Time to hatch, 3–4 days. The larvae eat more or less of the chorion.

Larva: first instar.—At hatch 1.6 mm long at rest. Dull yellow with a black head, becoming grayish-green with full pattern (see below) of longitudinal pale yellow stripes after feeding. Numerous black tubercles bearing pale hairs. Begins by excavating pits in buds, flowers, green fruit, or leaves. Length of instar, 2 days.

Second instar.—After molt 5 mm. Slate gray with yellow stripes as follows: a faint mid-dorsal line; stronger subdorsal; and stigmatal. Head slate gray. Ocelli and true legs black; venter and prolegs greenish-gray. Head and body with many black tubercles falling into 3 size classes, surmounted by whitish hairs. Length of instar, 2–3 days.

Third instar.—After molt 9.4 mm. Similar, the yellow dorsal line tending to disappear; feeds openly near top of plant on inflorescences and leaves. 3–4 days.

Fourth instar.—After molt 15.3 mm. As before, the mid-dorsal line often completely lost. 3–4 days.

Fifth instar.—After molt 25.4 mm, when full grown 34 mm. Head gray with many black tubercles, each bearing a whitish hair, and faintly mottled in orange. Body with the yellow dorsal line barely if at all visible within a broad dorsal stripe of gray ("grayish turquoise," 24E3); below this are greenish-yellow ("primrose yellow," 1A6) subdorsal stripes including two orange (6A6) dots and two large black tubercles on each segment; below this a gray (24E3) stripe and below it a yellow (1A6) stigmatal stripe containing two orange (6A6) dots, one anterior and one posterior to the spiracle; shading into blue-green ("greyish green," 25D5) which continues across the venter, including the prolegs. Body with numerous black tubercles as shown, some conical, each bearing a short whitish hair. The anterior ends of all of the yellow stripes on the prothorax are orange and expand to form a narrow orange "collar" directly behind the head.

Occasional aberrant larvae have been found in which the dark stripes are dark bluish green ("opaline green," 25C6) or else purplish gray ("dull violet," 16D3) with the light markings all orange (6A6). The former seems to be genetically determined, while the latter is associated with parasitism by the Braconid *Apanteles ayerzai* Brethes.

Mature larvae "stem" the hosts and sit on the bare stalk, where the striped pattern is highly cryptic. The final one or two fecal pellets are red. Length of instar, 6–7 days.

Prepupa.—Vertical, head up, attached in usual Pierid fashion by the anal prolegs and a silken girdle around the thorax. The color does not change conspicuously (unlike the genus *Euchloe* of the Holarctic, with a similar larva). Unlike most Pierines, the mature larva does not wander before pupation and usually attaches itself to the host, either on the bare stem or (if the host is quite leafy) on the underside of a leaf. 18–30 hours.

Pupa.—Length 24–25.5 mm, the female noticeably larger. Width at girdle

5–5.5 mm. Initially colored like the larva, assuming its final coloration in 4–6 h. Ground light pinkish gray ("pinkish white," 9A2) with numerous but inconspicuous black tubercles corresponding to those of the larva; dorsal midline strongly carinate on the thorax, with a series of black-tipped smaller keels anteriorly on the abdominal segments; frontal and supraocular prominences all the same size, black, 3 dorsolateral flaring prominences above the spiracles moderately developed, not marked with black; two rows of light orange dots, each with two to a segment, on either side of the dorsal midline and in line with the spiracles, corresponding to their larval positions although the yellow stripes containing them are essentially lost; eyes and appendage cases, including wings, light gray (7B1), unmarked except for a black spot at the end of the discal cell and tiny black dots along the outer wing margin. Spiracles black. Cremaster light gray. Thorax mottled dorsally with olivaceous gray ("brownish grey," 6C2); frons and vertex creamy white, contrasting. The color scheme of the pupa is invariant and reminiscent of *Pieris beckeri* Edwards of western North America. It is probably a bird-dropping mimic. The shape is more slender and angular than *T. xanthodice* Lucas (Shapiro 1978b).

Before eclosion the eyes, wings, and body are pigmented in that order. White is laid down 12–18 h before black. Meconium red. Length of instar 6–10 days.

Tatochila blanchardii Butler (Fig. 2)

T. blanchardii is the ecological equivalent of *autodice* in Chile, from Tarapacá (20°S) to Cautín (39°S) and crossing the Andes into the Argentine provinces of Chubut and Río Negro, including the Nahuel Huapí National Park and the Bariloche district, where *autodice* is a rare casual. In the Central Valley of Chile it is common in disturbed urban and agricultural habitats and breeds on the introduced Crucifers *Rapistrum rugosum*, *Sisymbrium officinale*, and *S. orientale* L. Herrera and Field (1959) and Peña (1975) suggest Tropaeolaceae as hosts, perhaps following Giacomelli (1915). *Tropaeolum majus* is accepted by the larvae.

The species is multivoltine, with about four generations per year at Santiago (September–May). At Bariloche, where it breeds on *Brassica geniculata* and *Sisymbrium officinale*, it has at least two generations with perhaps a partial third. Winter is spent as a diapausing pupa.

The following descriptions are based on a composite of material from the Chilean Central Valley (*leg.* Kellner) and bred *ex ovo* from Bariloche.

Descriptions

Egg.—Similar to *T. autodice*, slightly smaller, 1.10×0.30 mm, with 8–9 vertical and about 32 horizontal ribs. Laid singly on stems, fruits, flowers,

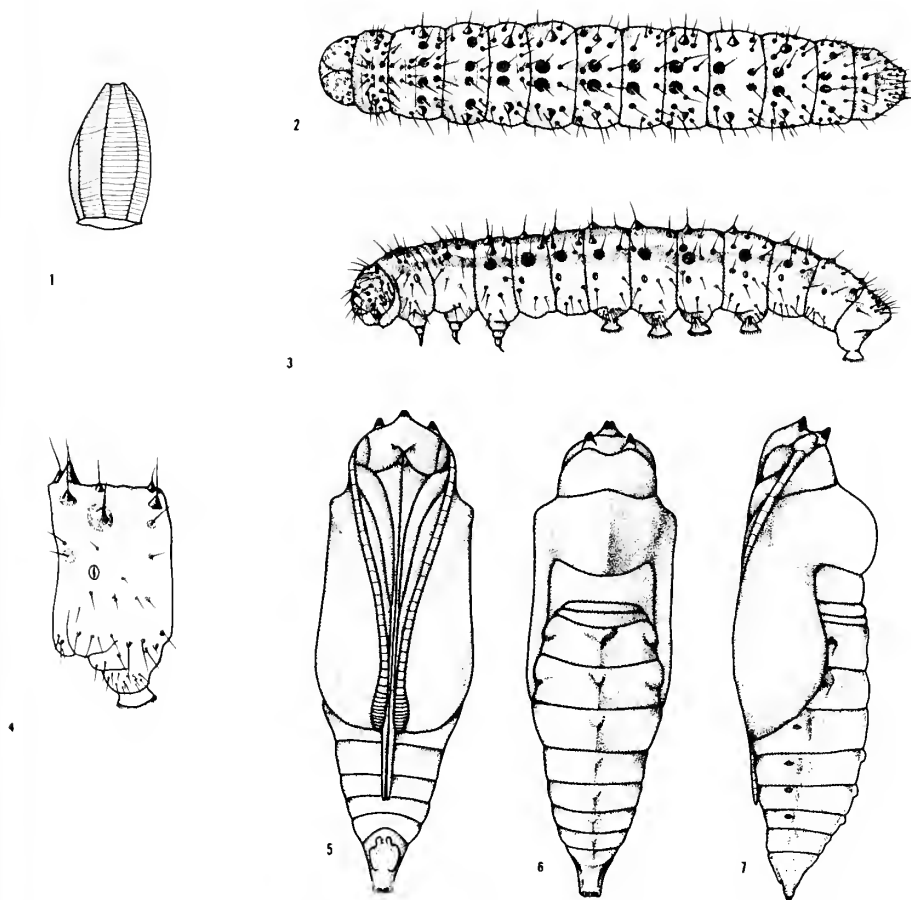


Fig. 2. *Tatochila blanchardii* from Santiago, Chile: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, lateral view of seventh segment, showing major tubercles; 5, pupa, ventral view; 6, pupa, dorsal view; 7, pupa, lateral view.

and indiscriminately on upper and lower surfaces of leaves. Usually laid on plants in at least partial shade. Light orange when laid, darkening to deep orange after 12–18 h, and to translucent blackish 12 h before hatch. 3 days.

Larva: first instar.—At hatch 1.5 mm at rest. Yellow, with black head; becoming dark gray-green with full *Tatochila* pattern after feeding. Length of instar, 2–3 days.

Second instar.—After molt 4.5 mm. Black, with a barely discernible yellow mid-dorsal line; two strong subdorsal yellow stripes; shading into gray from the spiracles across the venter, including the prolegs. Head dark gray, ocelli black. Tubercles as in *autodice* but more prominent, bearing whitish hairs; the largest with dark hairs. Length of instar, 3 days.

Third instar.—After molt 7 mm. Similar; resting for long periods on the stem, where highly cryptic. Length of instar, 3 days.

Fourth instar.—After molt 12.0 mm. As before. 3–4 days.

Fifth instar.—After molt 19 mm, reaching 29.5 mm when full-fed. The most slender *Tatochila* larva yet reared. Mustard yellow (2A6) with very prominent large tubercles as shown, bearing dark hairs; smaller tubercles in two sizes, less conical, bearing light hairs. With a narrow but well-defined mid-dorsal yellow line and subdorsal stripes, about three times as wide and of the same color (2A6); dark stripes purplish-gray (13D2), containing a row of very large tubercles directly above the spiracles; pleural and ventral areas light grayish yellow, the venter slightly green-tinged, separated by a diffuse purplish-gray line. Spiracles black. Head gray with irregular yellowish mottling and many black tubercles; ocelli black.

As in *T. autodice*, the larva eats all parts of the plant, “stemming” it. It rests low on the bare stem. The final one or two fecal pellets are red. Length of instar, 3–5 days.

Prepupa.—Vertical, head up, as in *T. autodice*; at Bariloche commonly on the host. Length of prepupal period 18–30 h.

Pupa.—Length 21 mm, width at girdle 6 mm (reared *T. b. ernestae* Herrera, from extreme northern Chile, average only 19×4.9 mm but do not differ in color and pattern). Similar to *T. autodice* in color and pattern, but slightly stockier; with broad olivaceous gray (6C2) stripes above the spiracles, dorsad of the flaring prominences, concolorous with the dorsal thoracic mottling. Meconium red. Length of instar, 7–12 days.

The *T. sterodice* Species-Group

This is a very homogeneous group of six named entities: *T. sterodice* with four subspecies, *T. vanvolxemii*, and *T. mercedis*. All of these are apparently allopatric (or in the case of *T. s. macrodice* and *T. vanvolxemii*, isolated by altitude). *T. sterodice* has the widest latitudinal range of any South American butterfly, from central Colombia (3°N) to Tierra del Fuego (55°S). The other species are confined to the temperate mid-latitudes.

All lay orange eggs, which differ among themselves in the sculpturing of the chorion; all are more fusiform than in the *autodice* group. All have stocky larvae and pupae, relative to that group. The larvae are striped lengthwise in black and yellow, generally with complete *Tatochila* pattern (yellow mid-dorsal line, subdorsal stripes and a broken stigmatal line which may be reduced to pairs of spots, one anterior to and one posterior to, each spiracle). When mature they are somewhat lighter in ground color and have a pronounced resemblance to some Noctuid “cutworm” larvae, from which they differ in having many black tubercles in three sizes, bearing light hairs. The pupae are smooth, without the abdominal keels and with only rudi-

mentary dorsolateral prominences, and resemble the pupa of *T. xanthodice* except for the much longer proboscis case in this group.

All the species are associated with weedy Crucifers in highly disturbed habitats, and are today mainly anthropophilic. No member of this species-group has been recorded on Tropaeolaceae to date. All known populations, except perhaps *T. s. fueguensis* from Tierra del Fuego, are at least bivoltine and overwinter as a pupa under photoperiod-temperature induced diapause (except *T. s. arctodice*, which breeds continuously).

Tatochila sterodice Staudinger

The four races of this Andean insect replace one another latitudinally and are associated with major physiographic-ecological regions: *T. s. arctodice* in the northern Andean *altiplano*, *T. s. macrodice* in the *puna*, *T. s. sterodice* in the Patagonian Andes, and *T. s. fueguensis* in the subantarctic forest region. The last two are probably clinal across southern Patagonia and the Isla Grande de Tierra del Fuego. The most distinct of the subspecies is *arctodice* Stgr., which is circumequatorial and uniquely in the group does not appear to diapause. Its biology was studied by Alvarez and Delgado (1969) and will not be repeated here. The other three subspecies all occur in Argentina; their early stages show no more differentiation than the adults.

Tatochila sterodice macrodice Staudinger (Fig. 3)

This subspecies was studied around Tañi del Valle, Province of Tucumán, in a dry-montane environment in one of the isolated ranges east of the Andes proper (27°S). It was found in vacant lot and roadside habitats, exploiting weeds such as *Descurainia argentina*, *Brassica geniculata*, and *Lepidium* sp. (? *ruderales* L.). In Salta and Jujuy it occurs above 3000 m (B. MacPherson, R. Eisele, *pers. comm.*) and perhaps has native non-weedy hosts. The range extends to southern Peru, extreme northern Chile, east into Bolivia and south in Argentina to Mendoza, where it may intergrade to the next. All records known to me are from above 1500 m.

Males are vigorous "hilltoppers." The behavior of this subspecies was described in detail by Jørgensen (1916). In northwestern Argentina its flight season is November to April, with two or three broods.

Descriptions

Egg.—Erect, fusiform, 1.15×0.40 mm, with about 16 vertical and 35 horizontal ribs. Bright orange when laid, scarcely darkening until 12 h before hatch when it becomes translucent blackish. Time to hatch, 5–6 days. The eggs are laid singly on stems, inflorescences, and cauline leaves of larger

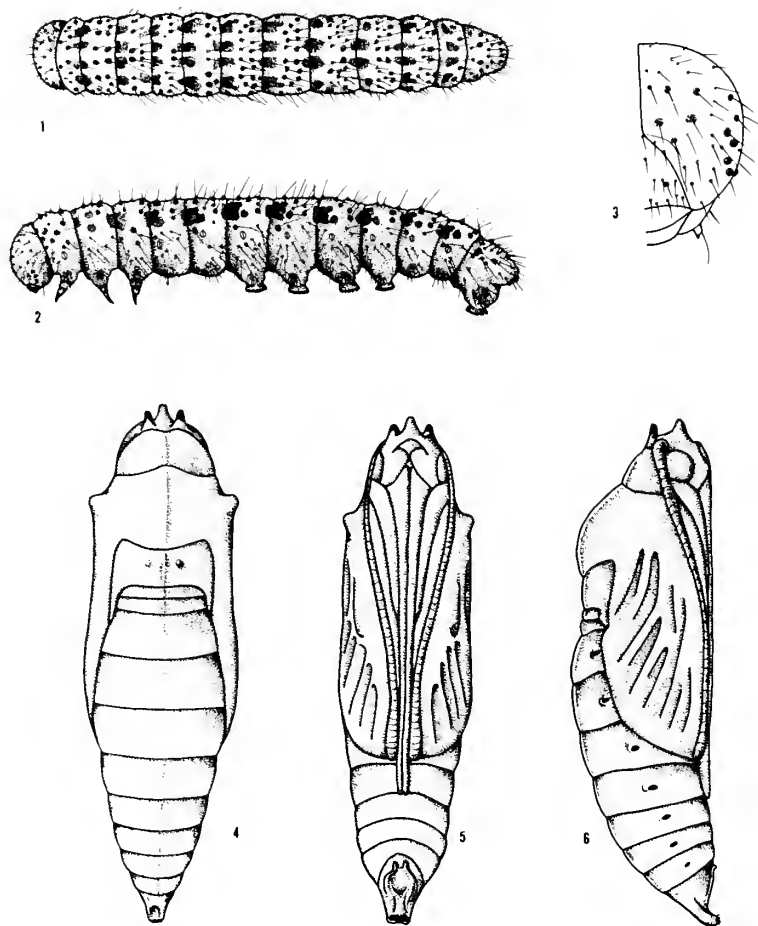


Fig. 3. *Tatochila sterodice macrodice* from Tafí, Tucumán, Argentina: 1, fifth instar larva, dorsal view; 2, fifth instar larva, lateral view; 3, mature larva, head capsule; 4, pupa, dorsal view; 5, pupa, ventral view; 6, pupa, lateral view.

plants, and also on the upper surfaces of small rosettes. More than half the eggs seen at Tafí were laid on apical buds.

Larva: first instar.—At hatch 1.4 mm. Pale yellow with dark brown head. After feeding olive green with the usual yellow pattern at first weakly, then more strongly indicated, with many black tubercles. The larva eats pits in soft tissue, preferably of buds. It eats its entire chorion. Time to molt, 2 days.

Second instar.—After molt 4 mm. Black, with lemon yellow stripes in the

full *Tatochila* pattern; tubercles, ocelli and spiracles black; venter gray. Length of instar, 2–3 days.

Third instar.—After molt 6.5 mm. Same pattern, with indistinct orange spots at the anterior end of each subdorsal yellow stripe on each segment, and on either side of each spiracle. Mid-dorsal yellow line strong. When not feeding the larva sits along the stem. 3 days.

Fourth instar.—Length after molt 10.5 mm. Subdorsal stripes less bold, the mid-dorsal one persistent. Length of instar, 4 days.

Fifth instar.—After molt 18.5 mm, reaching 30–32 mm at maturity. Body blackish gray ("medium grey," 1E1); mid-dorsal yellow line distinct, the subdorsal stripes less so but containing an orange spot at the anterior, and sometimes the posterior, end on each segment; a distinct orange spot anterior, and a less distinct one posterior to each spiracle; venter dull gray ("pastel grey," 1C1). Tubercles in 3 size classes, black, bearing light hairs. The stripes of ground color contain large squarish black spots anteriorly as figured, on the dorsum of each segment; they occur throughout the species-group. Larvae "stem" the host, sitting low on the leafless stalk, usually head down. The last fecal pellets are red. Length of instar, 6 days.

Prepupa.—Formed at some distance from the host, the larva wandering without feeding for 2–6 h. Time to molt, 14–27 h.

Pupa.—22.5 × 5.5 mm. Initially deep slate-green ("greyish green," 25D5); within 8 h turning light pearly gray ("reddish grey," 9B2); with numerous small black tubercles corresponding to their larval positions, but inconspicuous; dorsal and subdorsal lines as in the larva, whitish, the latter containing faint orange dots anteriorly on each segment; the orange amphispiracular spots also faintly indicated on the abdomen. Head and appendages—including wing-cases—ochreous ("greyish yellow," 4B4) with variable but rarely extensive black filling between veins on the outer half, and a black discocellular dot. Attached vertically, head up, on dry weeds, fence-posts, walls, etc. Pigment sequence as usual; meconium red; time to hatch, 8–13 days.

Some pupae of *T. s. macrodice* have a series of black dots anteriorly on the dorsal abdominal midline, corresponding to those in the *autodice* group.

Tatochila sterodice sterodice Staudinger (Fig. 4)

Cultures were established from localities near the northern and southern extremities of the range of this subspecies: San Carlos de Bariloche, Río Negro (41°08'S) and Río Gallegos, Santa Cruz (51°37'S), the latter transitional to *T. s. fueguensis* Field. No morphological differences were noted, but Río Gallegos stock grows more rapidly, its mean time from oviposition to eclosion being 3–4 days shorter. Data given below are for Bariloche, where the population is partially triple-brooded (October to March). At Río

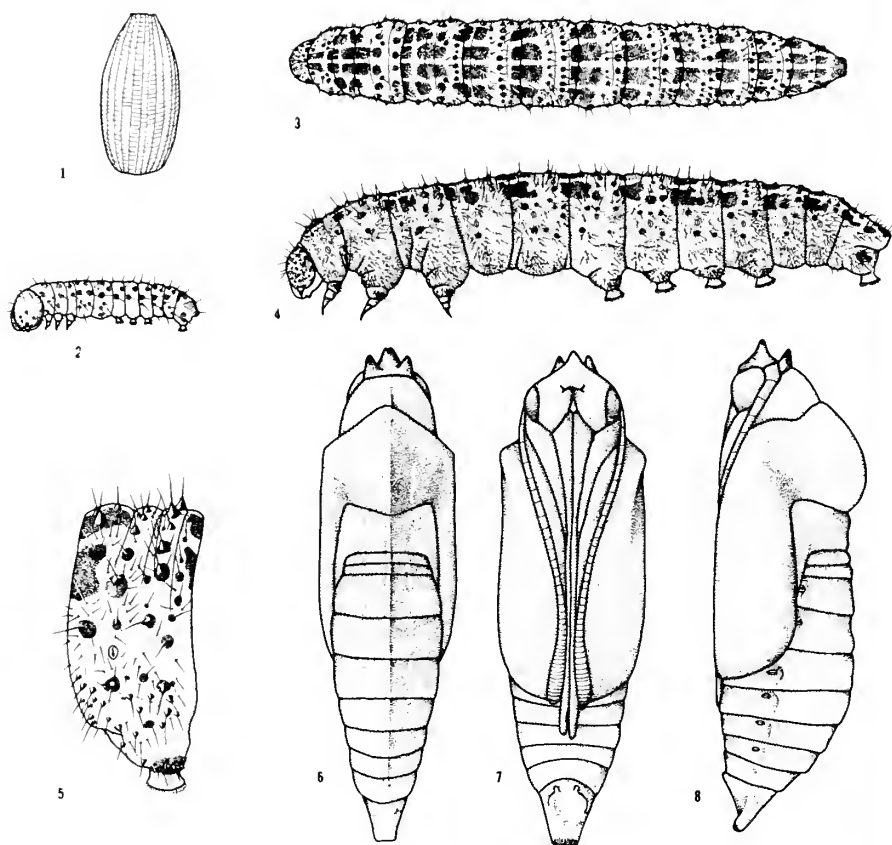


Fig. 4. *Tatochila sterodice sterodice* from Bariloche, Argentina: 1, egg; 2, newly hatched larva showing primary tubercles and setae; 3, mature larva, dorsal view; 4, mature larva, lateral view; 5, lateral view of seventh segment, showing major tubercles; 6, pupa, dorsal view; 7, pupa, ventral view; 8, pupa, lateral view.

Gallegos it is probably at least partially double-brooded (November–February). Winter is spent as a diapausing pupa. Although males “hilltop,” this subspecies is often found in areas of uniform low relief.

The recorded hosts are numerous and all of Palearctic origin: at Bariloche: *Rapistrum rugosum*, *Coronopus didymus*, *Lepidium rudemale*, *L. perfoliatum*, *Raphanus sativus*, *Brassica geniculata*, *B. campestris*, *Sisymbrium officinale*, and *S. irio*. At Río Gallegos: *Cardaria draba*, *L. perfoliatum*, *R. sativus*, *B. geniculata*, *B. campestris*, *B. kabera* (DC.) Wheeler, *S. officinale*, *S. altissimum* L., and *S. irio*. There are no native Crucifers on the Patagonian coast, where *sterodice* is common in all the larger towns.

Descriptions

Egg.—As in the preceding, 1.12×0.37 mm, with about 18 vertical and 35 horizontal ribs, dull orange when laid, darkening slightly after 6–12 h, becoming blackish-translucent 8–12 h before hatch. Laid singly on buds and stems of flowering plants and commonly on leaves of rosettes. Time to hatch, 6 days.

Larva: first instar.—At hatch 1.4 mm long. Pale yellow with brown head; after feeding olive green with the full yellow *Tatochila* pattern. Tubercles black. On flowering plants the larva consumes the buds; on rosettes it excavates pits. Time to molt, 4 days.

Second instar.—Length after molt, 3.9 mm. Olive green, the usual pattern yellow, with strong mid-dorsal and subdorsal lines and numerous black tubercles. Feeds by preference on flowers and young, green fruit. 3 days.

Third instar.—After molt 7.2 mm. Blackish olive ("greyish green," 28E5) with the full yellow pattern, including distinct amphispircular spots. 4–4.5 days.

Fourth instar.—After molt 10.5 mm. As before, the dark blotches on the anterior portion of each dorsum more conspicuous; orange spots at the anterior end of each subdorsal stripe on each segment, and on both sides of the spiracles. Time to molt, 5 days.

Fifth instar.—After molt 17 mm, reaching 28 mm. Olivaceous gray-green ("olive," 3E6) with a well-defined mid-dorsal and pair of subdorsal lines, all of about equal width, yellow; an orange dot within each subdorsal line at the anterior end of each segment; orange dots anterior and posterior to each spiracle (in about 40% of larvae these dots are yellow); subspiracular area and venter, including prolegs, greenish gray (1D2); head brownish-gray mottled with orange, tubercles and ocelli black. Body with many tubercles falling in three size classes, surmounted by fine pale hairs.

The larva "stems" the plant and as usual sits lengthwise on the stem, head up or down. Last fecal pellets red. Time to molt, 7–8 days.

Prepupa.—Wandering for 3–8 h before spinning. Vertical, head up. 18–36 h.

Pupa.—Length 20.5–22 mm, width at girdle 5–6 mm. Initially slate green ("greyish green," 25D7), assuming its final coloration in 6 h. Colored exactly as in *T. s. macrodice*, generally with little black filling on the wing-cases. Dorsolateral prominences very weak. Frontal and supraocular prominences equal, black. Pre-hatch pigmentation sequence normal, meconium red. 8–15 days. This is the slowest-developing *Tatochila* yet reared.

Tatochila vanvolxemii (Capronnier) (Fig. 5)

Distributed in Argentina from the Province of Tucumán (27°S) to Río Negro and southern Buenos Aires (40°S) in subhumid to subarid grassland,

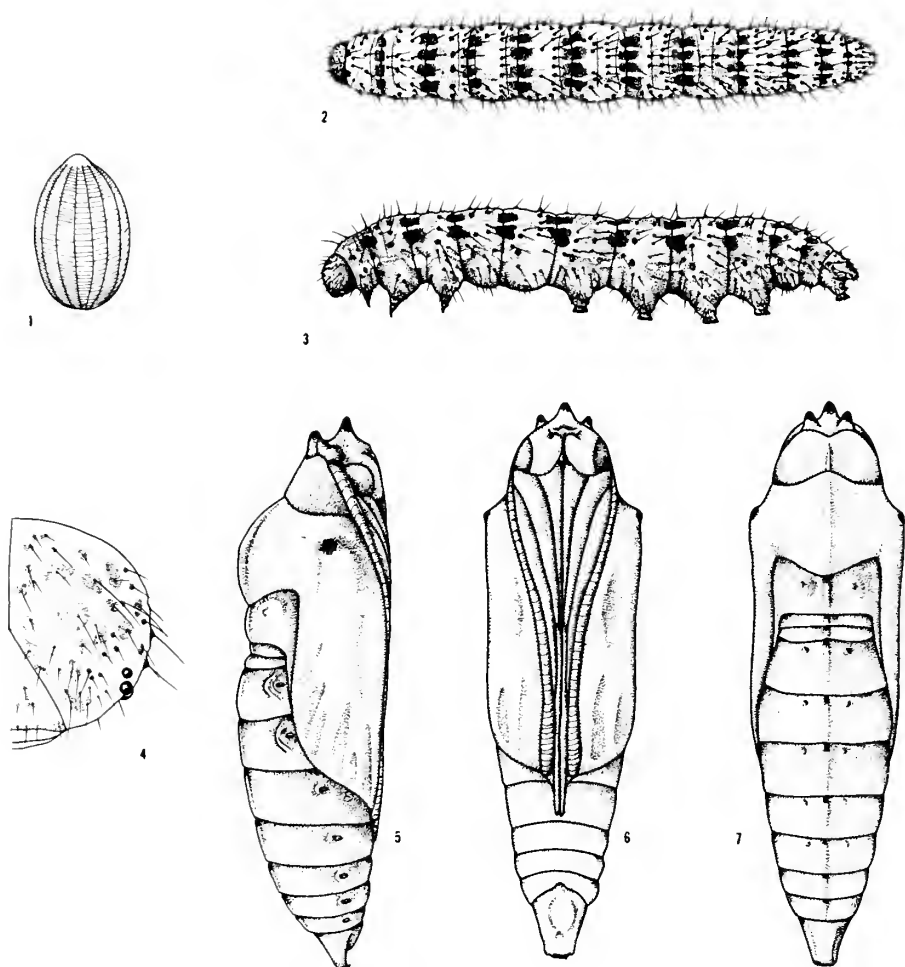


Fig. 5. *Tatochila vanvolxemii* from central Argentina: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, mature larva, head capsule; 5, pupa, lateral view; 6, pupa, ventral view; 7, pupa, dorsal view.

its ecological range almost exactly matching that of the North American *Pieris protodice* Bdv. & LeC. which it also resembles phenotypically. It is very abundant in disturbed sites and has been recorded on both native and introduced Cruciferous weeds: *Rapistrum rugosum*, *Coronopus didymus*, *Cardaria draba*, *Lepidium* (several species), *Descurainia appendiculata*, *Raphanus sativus*, *Brassica geniculata*, *Sisymbrium officinale*, *S. altissimum*, and *Eruca sativa*. Of these *B. geniculata* and the *Lepidium*s seem to be most often used. The species is 3–5-brooded in various parts of its range,

overwintering as a pupa in photoperiod-and-temperature-induced diapause. Jörgensen (1916) records it from early October to mid-May in Mendoza at 937 m. Primarily a lowland species, it does not appear to "hilltop."

Stocks were obtained from Córdoba and Capilla del Monte, Province of Córdoba (31°S) and Bahía Blanca, Province of Buenos Aires (38°44'S), near its northern and southern range extremities. No morphological or developmental differences were found. Both stocks are polymorphic for a number of adult and larval characters.

Descriptions

Egg.—Usual form, 1.2×0.33 mm, when laid light yellow to yellowish-orange, usually but not always darkening to deeper orange after 6 h (the difference appears to be hereditary through the female line); with 12–15 vertical and 34–37 horizontal ribs. Becomes opaque and hyaline 12 h before hatch. Laid singly on buds, fruit, stems or leaves. This species produces very large numbers of eggs per female, sometimes over 600 (Margheritis and Rizzo, 1965 quote a figure of 4–500 for *T. autodice*). Time to hatch, 3–4 days.

Larva: first instar.—At hatch 1.6 mm. Dull olivaceous-yellow, head black. Feeds preferentially on flowers, but will eat pits in leaves; becoming gray-green with full yellow pattern. 2 days.

Second instar.—3.3 mm after molt. Slate gray, with full yellow pattern and numerous black tubercles. Time to molt, 2–3 days.

Third instar.—Length after molt 9.5 mm. Slate gray with the usual yellow pattern of a mid-dorsal line and subdorsal lines, about twice as broad; a yellow spot anterior and posterior to each spiracle, the size and shape of these spots variable; four blackish blotches on the anterior dorsum on each segment, as illustrated; head gray, mottled with dull yellow, ocelli and tubercles black. Venter and prolegs gray. True legs and tubercles black, the latter in three size classes, bearing light hairs. Feeds on all parts of the plant. 3–4 days.

Fourth instar.—15.5 mm. Head gray, with a yellow cast. Yellow amphispiracular spots frequently connected to form a zigzag stripe. Faint orange spots occasionally present anteriorly in the subdorsal lines on each segment. The mid-dorsal line weak but still present. 3–4 days.

Fifth instar.—After molt 25 mm, reaching 33.5 mm. As before, the ground color becoming dingy mouse-brown ("greyish brown," 5D3), producing a very cutworm-like effect, with the black dorsal blotches strongly contrasting; the spiracular spots joined in a line in about 65% of the larvae, otherwise variously shaped, sometimes partly or all orange. As usual the larvae "stem" the host and sit on the bare stalk. The last fecal pellet or two are red. Time to molt, 5–7 days.

Prepupa.—Attached in the usual manner, vertical, head up, after a wandering period of 4–6 h or more. Duration of prepupal period, 12–20 h.

Pupa.— 21.5×5.6 mm. At first slate green ("greyish green," 25D7), within 6 h colored exactly as in *T. s. macrodice*; black filling on wing cases variable, rarely pronounced. Black dots on dorsal abdominal midline almost always present and conspicuous. Dorsolateral prominences very weak. Frontal and supraocular prominences equal, black. Eyes, wings and body become pigmented in that order; white is laid down 30 h, black 12 h, before eclosion, which is almost always within 30 min of sunrise. Meconium red. Length of instar 6–9 days.

Wild pupae occur on walls, fence posts, rubbish, and dry weeds and have not been found on the host. If *T. vanvolxemii* breeds on any of the Caparidaceous shrubs which occur in its range it might pupate on them.

Tatochila mercedis (Eschholtz) (Fig 6)

This small species is the most aberrant in the group. It occurs in Mediterranean Chile from Atacama to Llanquihue (27° – 41° S), generally in highly disturbed habitats in agricultural or waste ground on valley floors and in foothill canyon bottoms. It is multiple-brooded (August–April at Santiago; five broods?) and winters as a diapausing pupa. Its recorded hosts are *Rapistrum rugosum*, *Raphanus sativus*, *Brassica campestris*, *Sisymbrium officinale* and *S. orientale*. All of these are European, and Peña (1975) predicts that a native Chilean host will be found.

T. mercedis is occasionally recorded at Bariloche, Argentina (Herrera and Field 1959) and—obviously in error—in subtropical Misiones, northeast Argentina, by Breyer (1938). Giacomelli (1915) recorded it also from Bolivia, but there are no recent records from there.

Descriptions

Egg.—Similar to the others in this species-group but slightly smaller, 1.05×0.27 mm, with about 16 vertical and 33 horizontal ribs. Dull orange when laid, deepening in color after about 6 h; translucent blackish 12 h before hatch. Laid singly, mostly in inflorescences, but also on leaves of small rosettes. Time to hatch, 3–4 days.

Larva: first instar.—Dull yellow with black head; 1.05 mm at hatch. Feeds preferentially on buds, flowers or young fruit, but will excavate pits in leaves. Becoming gray-green with the usual yellow pattern after feeding; time to molt 2 days.

Second instar.—After molt 2.3 mm. Black, with the following yellow markings: a weak mid-dorsal line; a stronger, wider subdorsal stripe on each side; spots anterior and posterior to the spiracles. Head dark gray. Venter and prolegs dull greenish gray. Tubercles, prolegs and ocelli black. Length of instar, 3 days. (The spiracular spots may be orange.)

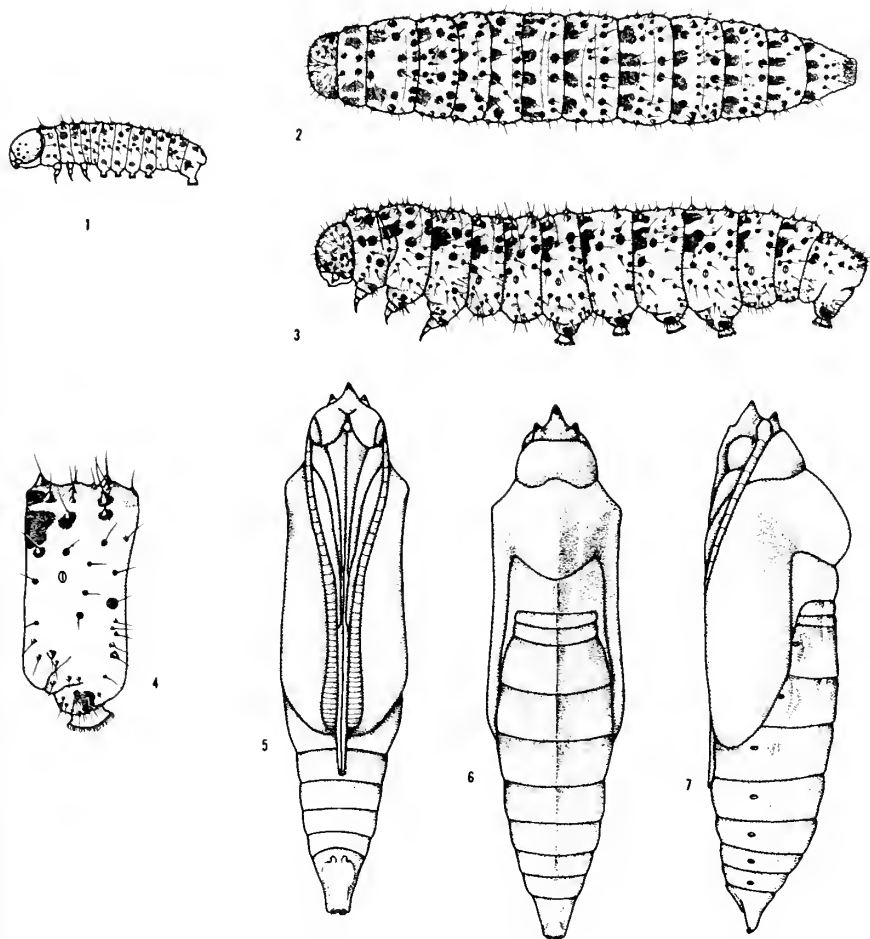


Fig. 6. *Tatochila mercedis* from central Chile: 1, newly hatched larva showing primary tubercles and setae; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, lateral view of seventh segment, showing major tubercles; 5, pupa, ventral view; 6, pupa, dorsal view; 7, pupa, lateral view.

Third instar.—After molt 4.2 mm. Pattern as before. Feeds in the open on the upper portion of the plant. Length of instar, 3–4 days.

Fourth instar.—Length 8.2 mm. Pattern as before, the dark blotches on the anterior dorsum of each segment becoming distinct. Tubercles conspicuous, black. 2–3 days.

Fifth instar.—15.5 mm, reaching 23 mm. Somewhat lighter, body gray-black ("medium grey," 1E1) with distinct black dorsal blotches as shown; usual pattern primrose yellow (1A6), the amphispiracular spots variable, sometimes connected in a zigzag line as in *T. vanvolxemii*, the dorsal midline

still visible but narrow. Venter dull gray ("pastel grey", 1C1). Head brownish-gray with a yellow cast. Tubercles, ocelli, and true legs black. The large tubercles are more conical in this species than in the others of the group, suggesting *T. blanchardii*.

Habits as in the other species, "stemming" the plant. Last fecal pellets red. Time to the prepupa, 6 days.

This description applies to larvae reared on slender Crucifers. When reared on heart leaves of cabbage (*Brassica oleracea* L.) lighter in color: ground brownish gray (7D3), the yellow markings paler and more extensive, making the tuberculation more contrasting.

Prepupa.—Head up, attached in the usual manner. Length of prepupal period, 14–20 h. Captive larvae wander for 3–6 h before spinning.

Pupa.—20 × 4.5 mm. Distinctively slender, but the dorsolateral prominences still weak. Frontal prominence often less blackened than the supraoculars, but of similar size. At first slate green ("greyish green," 25D7), but within 6 h turning buffy gray ("greyish orange," 5B3); wing-cases scarcely contrasting but sometimes slightly ochreous, without black filling between the veins; dorsal and subdorsal yellow lines preserved, along with numerous but inconspicuous black tubercles; spiracles black; a few black points along veins and wing margins, but little or no dark discal spot. Eyes, wings, and body pigmented in that order, white appearing 20 h, black 8–12 h, before eclosion. Meconium red. Length of instar, 8–11 days.

Discussion

Both species-groups recognized by Herrera and Field (1959) on adult characters are cohesive in their immature stages, as well.

The larval coloration of *Tatochila* seems very conservative. Within the *sterodice* group the differences among species are scarcely greater than those between subspecies. The most distinctive member of the group is *mercedis*, and its characters seem to bear on the evolutionary affinities between the *autodice* and *sterodice* groups.

Giacomelli (1915) derived the entire genus from *autodice*, making "*theodice*" (actually *blanchardii*) a very early offshoot, "*volxemi*" (*vanvolxemii*) next, then the *sterodice* group, even while admitting that "one must say in truth that *volxemi* is of doubtful placement and, more than all the other *Tatochila*, is of uncertain affinities." Giacomelli did not know the genitalic characters used by Herrera and Field (1959) in placing *vanvolxemii* solidly into the *sterodice* group (they found that the male genitalia of *sterodice* and *vanvolxemii* were indistinguishable). The early stages unambiguously support this judgment and at the same time suggest that the member of the group closest to *autodice* and *blanchardii* is not *vanvolxemii* but *mercedis*.

The dorsal pattern of both sexes of *autodice* and of the male *blanchardii* is a reduction of the full *Tatochila* pattern (still expressed in female *blan-*

chardii, and in males of ssp. *ernestae*). Of the other *Tatochila*, *mercedis* and some individual *sterodice* show the closest approximation to *autodice* dorsally. On the ventral hindwing, *autodice* and *blanchardii* almost always have an isolated spot in interspace Sc + R₁. Elsewhere in the genus this spot appears frequently in *mercedis* and occasionally in *sterodice* and nowhere else. In both it is usually connected to the vein. It represents pigment deposition in an aborted vein trace and may imply a phylogenetic connection between the *autodice* group and *mercedis-sterodice*. (This must be interpreted with caution; the same spot appears, obviously independently, in some stocks of Nearctic *Pieris napi* (L.)!) This hint is borne out in the larvae and pupae of *mercedis*—in the prominence of conical subdorsal tubercles on the larva, suggestive of *blanchardii*, and in the slender pupal shape.

T. mercedis is confined to Chile, a fact which bears on the direction of evolution in these groups. Due to its isolation Chile has a depauperate butterfly fauna (Peña, 1975) mostly derived from the Andes. With *sterodice* so widely distributed in the Andes it would more likely be ancestral to *mercedis* than the reverse; if the *mercedis-autodice* group connection is real, the likelihood that the *sterodice* complex *in toto* is derived from the *autodice* group is very low. Thus evolution is more likely to have proceeded from the *sterodice* to the *autodice* group than the reverse (as postulated by Giacomelli). *T. s. arctodice* of the northern Andes is phenotypically very close to the sympatric *T. xanthodice*, which on genitalic grounds is grouped by Herrera and Field (1959) with *T. distincta* Jörg. in a separate species-group. The early stages of *xanthodice* and of the *sterodice* group are also very similar, differing primarily in the number of ribs in the egg and the length of the pupal proboscis-case. Tentatively these two species-groups may be considered close, and primitive relative to the *autodice* group.

Parallel and convergent adaptations occur repeatedly in the Holarctic and Andean Pierid faunas. The rounded, stocky pupae of the *sterodice* group are approached by the montane and alpine members of the Holarctic *Pieris* (*Synchlœ*) *callidice* Hbn. complex. The striped pattern is a very widespread one in the family, but there is an almost uncanny resemblance among the mature larvae of *Tatochila autodice*, *Pieris protodice*, and the Eulichloine *Euchloe ausonides* Lucas. The angular pupa of the *autodice* group is similar in shape to the Holarctic *Pieris rapae* (L.) and *P. napi* (L.) species-groups, but less extreme than the latter. In South America this trend is carried to its apex in *Ascia monuste* (L.), in which the dorsolateral prominences are prolonged into curving black spines. The angularity of the pupa in Pierini seems very broadly correlated with environmental humidity, but there are too many exceptions to make this a cause-and-effect argument. "Bird dropping mimicry" occurs in the pupae of *Pieris beckerii* Edw. in western North America, and in *A. monuste*, which like *T. autodice* often pupates on the host. In subsequent phenetic or cladistic analysis of Pierini, including life

history traits, it will be necessary to keep in mind that bewildering, non-concordant parallelisms occur again and again in Pierine evolution (as noted for adult characters by Field (1958).)

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A RECONSIDERATION OF THE GENUS *BAKERIELLA*
(HYMENOPTERA: BETHYLIDAE)

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Abstract.—The concept of the neotropical genus *Bakeriella* is broadened to include several species formerly included in *Epyris*. Three species are described as new: *erythrogaster* (Costa Rica), *quadriceps* (Colombia), and *grandis* (Costa Rica). Females of *polita* Evans and *inconspicua* Evans are described for the first time. Range extensions for several other species are given. The 18 known species collectively range from Florida and Central Mexico to Brazil and Argentina.

Introduction

The genus *Bakeriella* was described in 1910 by Kieffer to include two South American bethylids related to *Epyris* but having pronotal carinae laterally, medially, and anteriorly. In 1964 I pointed out that there are similar species having the lateral and median carinae evanescent or even absent, and I redefined the genus to include these species. In my revision of *Epyris* (1969) I pointed out the close resemblance of members of the *montivagus* group of that genus to the species of *Bakeriella*. In fact, I suggested that the *montivagus* group might more properly be shifted to *Bakeriella* despite the lack of even the anterior pronotal carina in that group. Study of further material has convinced me that this step is inevitable, and furthermore that *Bakeriella* has evolved from a *Rhabdepyris*-like stock quite independently of *Epyris*. One species, described below as *erythrogaster*, in fact lacks a dividing septum in the scutellar groove, and thus will key to *Rhabdepyris* in most keys, although in all other features it is a true *Bakeriella*.

I believe that *Bakeriella* so redefined is a natural group, now known to contain 18 species collectively ranging from Florida and central Mexico to Brazil and Argentina. I present here a brief diagnosis of the genus as now conceived, a key to species, and remarks on each of the species, including a description of three new species and of the first known females of two others.

Generic features.—Epyrini fully winged in both sexes and with venation similar to that of *Epyris*. Antennal scrobes of female not carinate, but males

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with a delicate carina crossing above the antennal insertions and extending nearly to the lower eye margins; male antennae with dense erect or suberect setulae, third segment at least nearly as long as second. Eyes of female sparsely hairy, those of male barely or not at all hairy. Pronotum with a punctate groove paralleling the posterior margin, the disc prominent anterolaterally and often with a transverse carina connecting the anterior angles; sides of pronotal disc usually abrupt, often subcarinate or carinate; midline also sometimes carinate. Notauli strong on posterior half of mesoscutum; scutellum with a transverse basal groove which is usually divided by a thin septum, but sometimes undivided or divided by a flat-topped ridge. Propodeal disc elongate, tricarinate, the lateral discal carinae somewhat bowed, space between the carinae often transversely ridged; posterior angles of propodeum foveolate. Mesopleura with a single large fovea, the upper margin of which crosses above the pit. Middle tibiae of female spinose above.

Grouping of the species.—The following represents what I believe to be a natural grouping of the known species. I regard group I as most *Rhabdepyris*-like, group IV the most highly evolved in terms of thoracic sculpturing. In each case I have indicated which sexes have been described; at present 4 species are known only from females, 7 only from males.

Group I. Pronotum ecarinate. Scutellar groove simple.

1. *erythrogaster* n. sp. ♀ ♂

Group II. Pronotum ecarinate. Scutellar groove divided.

2. *montivagus* (Kieffer) ♀ ♂

3. *reclusus* (Evans) ♀ ♂

4. *quinquepartitus* (Kieffer) ♀

5. *quadriceps* n. sp. ♀

6. *grandis* n. sp. ♂

Group III. Pronotum with transverse carina. Scutellar groove divided.

7. *polita* Evans ♀ ♂

8. *rufocaudata* Evans ♂

9. *rossi* Evans ♂

10. *brasiliana* Evans ♀

11. *floridana* Evans ♀ ♂

12. *inconspicua* Evans ♀ ♂

13. *olmeca* Evans ♀ ♂ (Male has a weak median pronotal carina)

Group IV. Pronotum with transverse and median carinae. Scutellar groove divided.

14. *inca* Evans ♀

15. *azteca* Evans ♂

16. *depressa* Kieffer ♂

17. *flavicornis* Kieffer ♂

18. *cristata* Evans ♀ ♂

Key to Species

Females

1. Pronotum without a transverse carina 2
- Pronotum with a transverse anterior carina 6
2. Scutellar groove not divided by a septum; claws strongly curved, trifid 1 *erythrogaster* n. sp.
- Scutellar groove divided by a septum; claws moderately curved, dentate 3
3. Clypeus very short, subtruncate; posterior angles of head prominent and with a welt-like elevation 5 *quadriceps* n. sp.
- Clypeus angulate or subangulate medially; head rounded above eyes 4
4. Pronotal disc alutaceous, weakly punctate; scutellar pits only slightly wider than long 3 *reclusus* (Evans)
- Pronotal disc with weak surface sculpturing and rather strong punctures; scutellar pits much wider than long 5
5. Pronotal disc moderately shining, more strongly alutaceous than front and vertex, somewhat parallel-sided; propodeal disc slightly longer than wide 4 *quinquepartitus* (Kieffer)
- Pronotal disc shining, not or barely more alutaceous than front and vertex, shorter and with the sides more divergent behind; propodeal disc as wide as or slightly wider than long 2 *montivagus* (Kieffer)
6. Pronotum without a median carina; head black 7
- Pronotum with a complete median carina set off by linear grooves; or with a partially developed median carina, in this case the head dark green 11
7. Legs wholly testaceous; propodeal disc covered with weak transverse striations 11 *floridana* Evans
- Coxae and femora largely fuscous; sides of propodeal disc shining and with at most very weak sculpturing 8
8. Pronotal carina weakly angled forward medially; median area of propodeum rather weakly sculptured 9
- Pronotal carina evenly arched; median area of propodeum with strong transverse ridges 10
9. Mandibles with 5 teeth, the basal 3 small; front with small punctures which are separated by 1.5–3.0× their own diameters 13 *olmeca* Evans
- Mandibles with only two large apical teeth; front with somewhat stronger and more widely spaced punctures 10 *brasiliانا* Evans
10. Length of fore wing about 3.8 mm; sides of pronotal disc subcarinate anteriorly 7 *polita* Evans
- Length of fore wing about 3.2 mm; sides of pronotal disc carinate on anterior half 12 *inconspicua* Evans

11. Median carina of pronotum complete; head black; scutellar pits separated by a thin septum 14 *inca* Evans
- Median carina weakly developed on posterior third of pronotum; head with dark, metallic green reflections; scutellar pits separated by a flat-topped ridge 18 *cristata* Evans

Males

1. Pronotum without a transverse carina 2
- Pronotum with a transverse anterior carina 5
2. Scutellar groove not divided by a septum; claws trifid 1 *erythrogaster* n. sp.
- Scutellar groove divided by a septum; claws dentate 3
3. Abdomen rufous except basal segment largely black; length of fore wing 5.6 mm; propodeal disc slightly longer than wide 6 *grandis* n. sp.
- Abdomen black except extreme tip sometimes rufous; fore wing 2.5–4.0 mm; propodeal disc slightly wider than long 4
4. Front polished, very obscurely alutaceous and weakly punctate; notauli somewhat widened behind, but much more widely separated than their own greatest widths 2 *montivagus* (Kieffer)
- Front moderately alutaceous, rather weakly shining; notauli wide behind, separated by about their own greatest widths 3 *reclusus* (Evans)
5. Pronotum without a median carina 6
- Pronotum with a median carina (sometimes rather weak) 10
6. Front and pronotal disc polished, barely if at all alutaceous; larger species, fore wing 2.8–4.0 mm 7
- Front somewhat alutaceous, pronotal disc weakly shining, strongly alutaceous; smaller species, fore wing less than 2.5 mm in length 9
7. Antennae elongate, segment 11 at least twice as long as wide; apical 0.4 of abdomen rufous 8 *rufocaudata* Evans
- Antennae somewhat shorter, segment 11 not more than 1.7× as long as wide; tip of abdomen at most weakly suffused with reddish brown 8
8. Vertex rather narrowly rounded off far above eye tops; median lobe of clypeus roundly subangular 7 *polita* Evans
- Vertex more broadly rounded off, not so strongly angular 9 *rossi* Evans
9. Sides of pronotal disc subparallel, carinate anteriorly; coxae and femora fuscous 12 *inconspicua* Evans
- Sides of pronotal disc diverging behind, not at all carinate; legs bright testaceous except front coxae infuscated 11 *floridana* Evans
10. Temples not carinate 11
- Temples with a strong carina extending from vertex to near mandibular bases 12

11. Scutellar pits separated by a thin septum; pronotal disc subcarinate laterally, with a strong median carina 15 *azteca* Evans
 - Scutellar pits separated by a flat-topped ridge; pronotum rounded laterally, with a weak median carina 18 *cristata* Evans
12. Median carina of pronotum very weak; minimum width of front about $1.2\times$ eye height 13 *olmeca* Evans
 - Median carina of pronotum strong; minimum width of front barely if at all exceeding eye height 13
13. Transverse pronotal carina with the crest somewhat sinuate as seen obliquely from behind, subdentate on the sides 16 *depressa* Kieffer
 - Transverse pronotal carina with the crest rather even, not subdentate 17 *flavicornis* Kieffer

1. *Bakeriella erythrogaster* n. sp.

Holotype.—♀, COSTA RICA: Monte Verde, 13–15 Feb. 1972 (H. M. Powell) [Univ. Calif. Davis].

Description of female type.—Length 5.0 mm; fore wing 3.8 mm. Head and thorax black; abdomen bright rufous except basal segment partially suffused with black; mandibles castaneous; antennae light brown except darker on upper surface of flagellum; coxae and femora fuscous, remainder of legs medium brown; front wings uniformly tinged with brownish. Entire body strongly shining, with scattered short, brownish hairs, somewhat dense on head, pronotum, and femora. Mandibles with 4 teeth in an oblique series, the basal two teeth smaller and more rounded than the others. Median lobe of clypeus obtusely angulate, with a median carina which is straight in profile. Head $0.86\times$ as wide as high; width of front $1.4\times$ eye height; ocelli in a compact triangle far above eye tops, ocello-ocular line $2.2\times$ width of ocellar triangle. Eyes somewhat bulging from sides of head; vertex strongly arched, distance from eye tops to vertex crest (lateral view) subequal to eye height. Front very weakly alutaceous, with strong punctures which are separated by $2\text{--}5\times$ their own widths. Pronotum elongate, disc somewhat prominent anterolaterally; scutellar groove undivided, slightly widened on each side. Propodeal disc very slightly longer than wide, with a strong median carina that extends down the declivity; disc with two additional shorter carinae which are bowed in the form of a lyre, surface between these weakly and irregularly transversely striate, disc elsewhere with only very weak surface sculpturing. Claws strongly curved, trifid.

Allotype.—♂, COSTA RICA: Same data as type but dated 29 June 1972 [Univ. Calif. Davis].

Description of male allotype.—Length 4.0 mm; fore wing 3.5 mm. Color as in female except basal third of abdomen extensively suffused with black, antennae rather uniformly medium brown; body shining and with short, light brown hairs as in female. Mandibles with a strong apical tooth and 4 much

smaller teeth in a nearly straight series based at this tooth; clypeus as in female. Head $0.89\times$ as wide as high; width of front $1.1\times$ eye height; ocelli rather large, ocello-ocular line $1.3\times$ width of ocellar triangle. Antennae elongate, first 4 segments in a ratio of 12:7:8:10, segment 3 about $1.5\times$ as long as wide, segment eleven $3\times$ as long as wide. Eyes strongly bulging, not hairy, vertex broadly rounded off far above eye tops. Front very weakly alutaceous, its punctures smaller and sparser than in female. Features of thorax and propodeum as in female; claws trifid as in that sex.

Paratypes.—12 ♀♀, 2 ♂♂. COSTA RICA: 1 ♀, same data as allotype [Univ. Calif. Davis]; COLUMBIA: 11 ♀♀, 2 ♂♂, Peñas Blancas, Dept. Valle, 24 March 1975 (except 1 ♀ 22 Nov. 1974) (R. Wilkerson, Malaise trap) [Fla. State Coll. Arthropods; U.S. National Museum; Mus. Comp. Zool.].

Variation.—The Costa Rica paratype is closely similar to the type. The females from Colombia consistently have the basal two abdominal segments black, while the males have the greater part of the abdomen black, only the apical 2–3 segments rufous. In some of the females the basal mandibular tooth is partially divided, such that the mandibles are indistinctly 5-toothed. Some of the Colombia females are somewhat larger than those from Costa Rica, fore wing up to 4.5 mm. The head is consistently shorter in Colombia specimens than in those from Costa Rica, the head being from 0.88 to $0.92\times$ as wide as high in the females, from 0.94 to $0.96\times$ as wide as high in the males. However, there seems no basis for regarding these two series as representing different species or, in the absence of material from other localities, different subspecies.

Remarks.—This species will run to *Rhabdepyris* in existing keys because of the undivided scutellar groove. However, it fits poorly in that genus on other features and is quite clearly related to the more generalized species of *Bakeriella*.

2. *Bakeriella montivaga* (Kieffer) new combination

Epyris montivagus Kieffer, 1910; Evans, 1969.

This is possibly the most common and widely distributed member of the genus, ranging from Bolivia to Venezuela and to southern Mexico. Synonymy and a redescription are provided by Evans (1969).

3. *Bakeriella reclusa* (Evans) new combination

Epyris reclusus Evans, 1969.

This species was described from Costa Rica and El Salvador. I have since seen a female from ECUADOR: 11 km SE San Lorenzo. Prov. Esmeraldas, 1975 (S. & J. Peck) [Mus. Comp. Zool.].

4. *Bakeriella quinquepartita* (Kieffer) new combination

Epyris quinquepartitus Kieffer, 1910; Evans, 1969.

A redescription of this species was presented in 1969. Only the type female, from Marcapata, Peru, is known.

5. *Bakeriella quadriceps* n. sp.

Holotype.—♀, COLOMBIA: Finca los Guaduales, near San Jose del Palmar, Choco, 730–800 m, 1 June 1978 (C. Kugler) [Mus. Comp. Zool.].

Description of female type.—Length 5.2 mm; fore wing 3.5 mm. Head and thorax black; basal two abdominal segments black, third segment black except rufous along posterior margin, fourth segment partially suffused with black dorsally, remainder of abdomen bright rufous; mandibles dull ferruginous, black at base; antennae uniformly dull ferruginous; legs black except trochanters, tibiae and tarsi dusky ferruginous; wings subhyaline. Front with numerous short, golden brown setae, temples and thoracic dorsum and pleura more sparsely setose. Mandibles much broadened apically, with 4 large teeth, most basal teeth partially subdivided. Clypeus with a very short, broad truncate median lobe, its median line weakly carinate. Head quadrate, its posterior angles prominent and with a rounded welt; head very slightly higher than wide; width of front $1.4\times$ eye height; front angle of ocellar triangle less than a right angle, ocelli far below vertex crest, ocello-ocular line $2.3\times$ width of ocellar triangle. First 4 antennal segments in a ratio of 25:6:5:6, segment 3 about as wide as long. Eyes weakly hairy; distance from eye tops to vertex crest exceeding eye height; vertex nearly straight in anterior view for a considerable distance. Front alutaceous, moderately shining, with shallow punctures which are separated by $3\text{--}7\times$ their own diameters. Pronotal disc somewhat flat, prominent anterolaterally, surface somewhat more alutaceous and weakly punctate than that of front; scutellar pits slightly wider than long, separated by a thin septum medially. Propodeal disc distinctly widened posteriorly, length slightly exceeding its maximum width; median area with delicate, irregular transverse striae. Claws dentate.

Remarks.—This species is known only from the type.

6. *Bakeriella grandis* n. sp.

Holotype.—♂, COSTA RICA: Monte Verde, 29 June 1972 (H. M. Powell) [Univ. Calif. Davis].

Description of male type.—Length 8.0 mm; fore wing 5.6 mm. Head and thorax black; abdomen bright rufous except first segment largely suffused with black; mandibles rufous above and on apical half; antennae rufous except scape somewhat infuscated and apical third of flagellum fuscous; coxae and femora black, legs otherwise rufotestaceous except trochanters

and tibiae slightly infuscated; wings lightly and uniformly tinged with brown. Body and legs with fairly abundant short, light brown hairs. Mandibles with a large apical tooth and 4 very small teeth basad of this. Median lobe of clypeus angulate, tectiform. Head $0.95\times$ as wide as high; width of front $1.3\times$ eye height; ocelli in a compact triangle far above eye tops, ocello-ocular distance $1.55\times$ width of ocellar triangle. First 4 antennal segments in a ratio of 14:6:7:9, segment three $1.7\times$ as long as wide. Distance from eye tops to vertex crest subequal to eye height; vertex broadly arched. Front polished, very weakly alutaceous, punctures very small, separated by 4–6 \times their own diameters. Pronotal disc slightly duller and more alutaceous than front, but similarly punctate; pronotum prominent anterolaterally but without carinae. Notauli strong, extending for length of mesoscutum; scutellar groove rather wide, with a thin septum medially. Propodeal disc $0.95\times$ as wide as long, surface rather shining and with very weak surface sculpturing even between the carinae. Mesopleura punctate and with somewhat irregular sculpturing. Claws dentate.

Remarks.—This striking species is known only from the type.

7. *Bakeriella polita* Evans

Bakeriella polita Evans, 1964.

I described this species from males from Bolivia and Peru. I take this opportunity to describe a female from PERU: Monson Valley, Tingo Maria, 26 October 1954 (E. I. Schlinger & E. S. Ross) [Calif. Acad. Sci.].

Description of female.—Length 6.0 mm; fore wing 4.8 mm. Black, except apical third of abdomen suffused with dull rufous; mandibles and antennae ferruginous; coxae and femora fuscous, legs otherwise dull ferruginous; wings subhyaline. Mandibles 5-toothed; clypeus obtusely angulate, with a sharp median carina. Width of head $0.90\times$ length of head; width of front $1.25\times$ height of eye; ocello-ocular line $1.9\times$ width of ocellar triangle. Third antennal segment about as wide as long. Vertex broadly rounded off well above eye tops, top of occipital carina visible in full frontal view. Front polished, very weakly alutaceous, with strong punctures which are separated by 3–5 \times their own diameters. Pronotal disc similarly punctate but more distinctly alutaceous; front margin with a strong, evenly arched carina, side margins sharp but not carinate. Scutellar pits only slightly wider than long, septum between them round-topped, somewhat wider than in related species. Propodeal disc $1.15\times$ as wide as long, the median area with rather strong transverse rugae. Claws dentate.

8. *Bakeriella rufocaudata* Evans

Bakeriella rufocaudata Evans, 1964.

This species is known from a single male from the mountains of Colombia.

9. *Bakeriella rossi* Evans

Bakeriella rossi Evans, 1964.

I have seen no additional specimens of this species, described from males from two localities in Colombia.

10. *Bakeriella brasiliiana* Evans

Bakeriella brasiliiana Evans, 1964.

This species is evidently widely distributed in the neotropics. A female from the Chagres River, PANAMA, collected 14 July 1918 by Dietz & Zetek [U.S. Nat. Mus.] represents a considerable range extension.

11. *Bakeriella floridana* Evans

Bakeriella floridana Evans, 1964; Evans, 1970.

This small but distinctive species was described from Dade Co., Florida, and later reported from Good Hope, Jamaica. Presumably it will be found to occur elsewhere in the West Indies.

12. *Bakeriella inconspicua* Evans

Bakeriella inconspicua Evans, 1964.

I have seen several additional specimens of this species since the original description. A male from Tamazunchale, San Luis Potosi, MEXICO, collected 6 July 1965 (H. E. Evans) [Mus. Comp. Zool.] represents a small northward extension of the range. I have also seen a series of 1 ♀ and 6 ♂♂ from Merida, VENEZUELA, collected 17 November 1972 (G. E. Bohart) [Utah State Univ.]. Since this is the first female known, a short description follows.

Description of female.—Length 4.4 mm; fore wing 3.2 mm. Black, except apical fifth of abdomen bright rufotestaceous; apical half of mandibles ferruginous, antennae wholly of this color except apical segment dusky; legs fuscous except tarsi and parts of tibiae testaceous; wings hyaline. Mandibles with 3 strong teeth (may be 5-toothed); clypeus obtusely angulate, carinate medially. Width of head $0.87\times$ height of head; width of front $1.35\times$ eye height; ocello-ocular line $1.7\times$ width of ocellar triangle. Third antennal segment about as wide as long. Eyes slightly bulging, quite strongly hairy; vertex rounded off far above eye tops. Front shining, weakly alutaceous, punctures strong, separated by $2-4\times$ their own diameters. Pronotal disc more strongly alutaceous than front and with sparser punctures; disc with a strong, arching carina in front and the sides carinate on the anterior half. Scutellar pits ovoid, separated by a thin septum. Propodeal disc very slightly

longer than wide, its median area with irregular transverse rugae. Claws simple.

13. *Bakeriella olmeca* Evans

Bakeriella olmeca Evans, 1964.

This species was described from Veracruz, MEXICO. I am now able to present several additional records: BELIZE: 2 ♀♀, Middlesex, March 1965 (E. C. Welling) [Canad. Nat. Coll.]; NICARAGUA: 1 ♀, Musawas, Waspuc R., 23 October 1965 (B. Malkin) [Univ. Calif. Berkeley]; COSTA RICA: Osa Peninsula, Puntarenas (R. W. Matthews) [Mus. Comp. Zool.].

14. *Bakeriella inca* Evans

Bakeriella inca Evans, 1964.

This species was described from Peru, and can now be recorded from adjacent countries, as follows: ECUADOR: 1 ♀, Chimbaratzo, Zamora, 3, March 1965 (L. Peña) [Amer. Mus. Nat. Hist.]; BOLIVIA: 18 ♀♀, Rio Itenez, Beni, 1964 (Bouseman & Lussenhop) [Amer. Mus. Nat. Hist.]; 1 ♀, 20 km W Laranjeiras, August 1964 (Bouseman & Lussenhop) [Amer. Mus. Nat. Hist.].

15. *Bakeriella azteca* Evans

Bakeriella azteca Evans, 1964.

I have seen no additional specimens of this species described from a male from Morelos, MEXICO.

16. *Bakeriella depressa* Kieffer

Bakeriella depressa Kieffer, 1910; Evans, 1964.

I am unfamiliar with the female of this species, which was described from Peru and later reported from Panama and Costa Rica. I have also seen a male from ECUADOR: Puyo, 18 April 1958 (R. Hodges) [Mich. State Univ.].

17. *Bakeriella flavicornis* Kieffer

Bakeriella flavicornis Kieffer, 1910; Evans, 1964.

This species is known only from the type from Pará, Brazil. It is doubtfully distinct from the preceding species.

18. *Bakeriella cristata* Evans

Bakeriella cristata Evans, 1964; Evans, 1973.

I described this species from males from Brazil and Bolivia, and subsequently reported males from two localities in Argentina (in Salta and Misiones); I also described a female from Santa Catarina, Brazil. Evidently this distinctive species is widely distributed in South America.

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BOOK REVIEW

Diseases, Pests and Weeds in Tropical Crops. Jürgen Kranz, Heinz Schmutterer and Werner Koch, eds. John Wiley & Sons, 1978. 666 p. \$61.

This book has been prepared by more than 150 experts, but it appears homogenous because the contributors rigidly followed the same general outline. The volume contains an exhaustive number of fine illustrations, including numerous excellent color plates. The authors have succeeded in providing a text that is brief, readable, and authoritative. The information will be especially useful for those working in tropical Third World nations. Plant protection is emphasized throughout. The important pests and plant diseases are described in a way understandable not only by entomologists and plant pathologists, but also by students in agricultural colleges and lay persons. The work of many contributors has been sponsored by the German Government and a large number of contributors are from Central Europe. The paper as well as the printing and color reproduction, by Saledril Steinkopf & Son in Berlin, Germany, are of high quality. The book provides an important reference source and it belongs in every library in agricultural colleges and universities. There is an adequate subject index. Although the cited references indicate that it took 3–4 years to produce this book from submitted manuscripts, it is nevertheless up-to-date in most instances. The volume constitutes a major contribution to the crop protection literature.

K. Maramorosch, Waksman Institute of Microbiology, Rutgers—The State University.

BOOK REVIEW

American Spiders. (Second ed.) Willis J. Gertsch. Van Nostrand Reinhold Co. 1979. 274 p. \$24.95.

The first edition of this book appeared in 1949, with the description of nearly 3,000 species of American spiders. After 30 years the author revised his fascinating account, adding numerous new black and white photographs, 32 fine color illustrations, as well as descriptions of certain spiders living outside the New World. The book starts with an overview of the life of spiders, their silk spinning, courtship and mating, as well as the evolution of spiders and their relationship to other animals. The major groups of spiders—the mygalomorphs, to which the tarantulas belong, the Dribellate, aerial, and hunting spiders are all described. There is a very interesting chapter on the economic and medical importance of spiders. The book is not only authoritative but also quite readable and entertaining, thanks to anecdotes, myths, legends and beliefs. In addition to entomologists and students of spiders, everyone interested in natural history will find this volume stimulating and useful. The glossary and index are short but sufficiently detailed. Gertsch is meticulous about his facts and data and his contribution will be a welcome addition to college libraries and to personal libraries. It will appeal to lay persons as well as to science students, young and old, learned amateurs and professionals, as a fascinating account of the largely ignored, often feared, strange and complex spiders.

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VARIATION IN THE EMBOLUS OF *METAPHIDIPPUS*
INSIGNIS (BANKS) (ARANEAE: SALTICIDAE)

Bruce Cutler

Abstract.—Abnormal morphological variation in the emboli of male palpi of *M. insignis* from Minnesota and Montana is illustrated. Some of these emboli resemble normal emboli of *M. montanus*, a closely related species. This resemblance may lead to incorrect species determinations.

The palpus of the mature male spider is considered to offer the most consistent morphological elements for species discrimination. In some spider species parts of the palpus remain attached to the female epigynum as a normal consequence of mating (Exline and Whitcomb, 1965; Levi, 1970, 1973; McCrone and Levi, 1964). It is suspected in these species, that an individual female mates once or twice, and the loss of the male palpal elements prevents other males from mating with the same females. Since striking differences can occur in morphology between virgin and mated males, taxonomists must take this source of variation into account. However, since these parts break at the same points, and may be recovered from the epigyna, once this process is recognized little difficulty will be encountered in interpreting such variation taxonomically.

This paper describes a variation in palpal structure which is more difficult to explain, and may be taxonomically misleading. The embolus is the intermittent sclerite in male spiders. In the genus *Metaphidippus* it offers a reliable morphology for distinguishing species. Indeed it is almost the only criterion used to separate preserved male specimens, although differences may be subtle (Kaston, 1973). Figure 1A depicts a ventral view of the cymbium, bulb and embolus of a typical male *M. insignis* from Minnesota. This differs only slightly from the embolus illustrated by Kaston (1973). The embolus of *M. montanus* (Emerton), a closely related species, is shown in Figure 1B. The remaining figures are of aberrant emboli of specimens from Minnesota and Montana. The embolus illustrated in Figure 1C resembles that of *M. montanus* closely, yet the other palpus, body pattern, and body size are those of typical *M. insignis*.

Out of 39 male *M. insignis* taken in Minnesota, 9 exhibited at least one abnormal palpus. One example (not illustrated) had 2 extremely abnormal palpi in which all elements of the palpus were deformed. This may represent a true teratology, or may be the result of abnormal conditions during the final molt. There is no geographic clustering evident in these specimens, they come from all over the range of the species in the state. One gets the

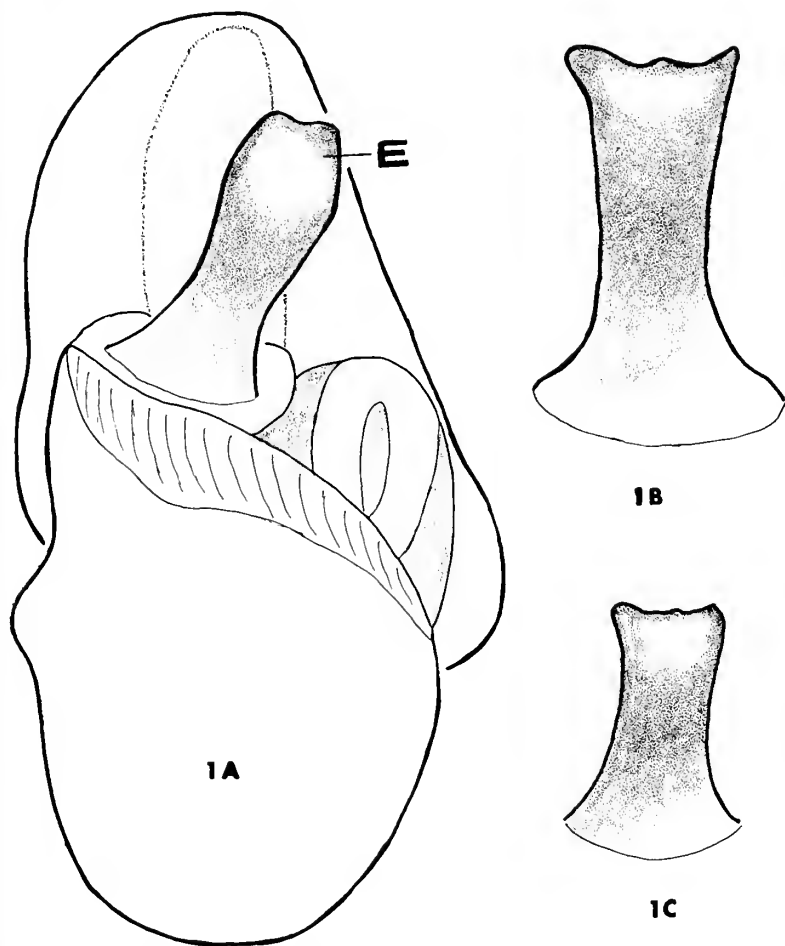


Fig. 1. A = Ventral view of typical left palpal tarsus of male *Metaphidippus insignis* from Minnesota, E is the embolus. B = Ventral view of left embolus of *Metaphidippus montanus* from Manitoba. C = Ventral view of aberrant left embolus of *Metaphidippus insignis* from Petroleum County, Montana.

impression that the typical rounded embolus tip has broken off to a variable degree producing the angular aberrant emboli. Over 50 females, including some collected at the same time as the males with atypical emboli, were examined. None had embolic remnants in the epigyna. I have also examined 4 males from Wyoming and Montana, and one of these has an abnormal embolus (Fig. 1C).

Kaston (1973) did not indicate any range of morphological variation in the emboli of *Metaphidippus* covered in his study. Galiano (1963) encountered

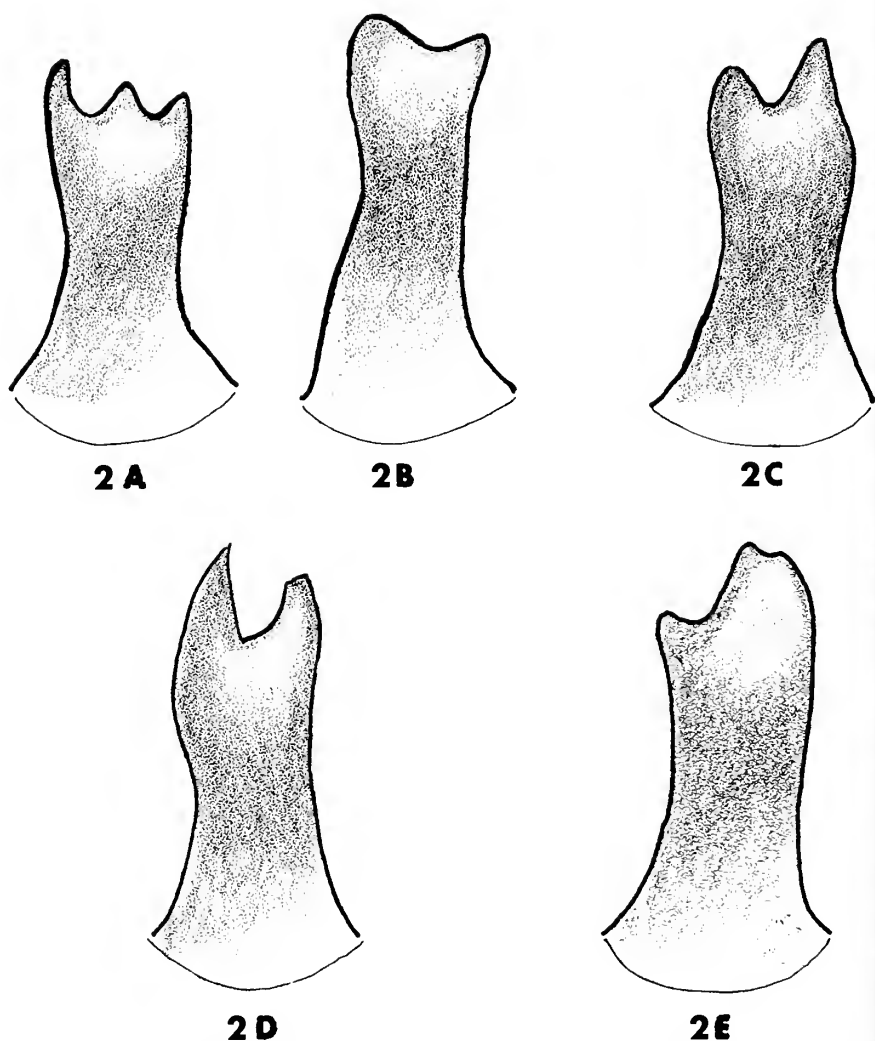


Fig. 2. Ventral views of aberrant emboli of *Metaphidippus insignis* from Minnesota. A = Left embolus of a male from Ramsey County. B = Right embolus of the same male as in A. C = Left embolus of a different male from Ramsey County. D = Right embolus of male from Ottertail County. E = Left embolus of another male from Ramsey County. Nonillustrated males similar to the illustrated specimens were from Norman, Pipestone, Stearns and Winona Counties.

an extreme range of variation in palpal morphology in male *Euophrys* (Salticidae) reared from one eggsac. Possibly some of this variation was the result of rearing. Male spiders often have difficulty in freeing the palpi during the final molt under laboratory conditions, although this usually affects the

structure of the other palpal elements rather than the embolus (personal observations). The few male *M. insignis* I have reared from wild caught immatures had typical palpi when mature. Perusal of the literature uncovered no species of jumping spider where a palpal element is broken off during mating.

I cannot explain the variations seen in *M. insignis*. I have examined hundreds of specimens of other species of *Metaphidippus* from Minnesota, and have never found any variation of the magnitude shown here in the emboli of these other species. It is possible that Minnesota and states to the west might lie in a hybrid zone between *M. insignis* and *M. montanus*. Unfortunately, few specimens are available from surrounding states and provinces to adequately study the problem.

M. insignis is found from New England and Ontario south to New Jersey, and west in the northern tier of states to the Rocky Mountains. In Minnesota, it is a grassland and meadow species, not found on primarily forested sites. *M. montanus* is found in the boreal forest from Newfoundland to the District of Mackenzie, and south in the high mountains of New England and New York. Many specimens determined as this species in collections, especially from the Rocky Mountains, belong elsewhere. It is a larger species than *M. insignis* with a slightly different body pattern. All known eastern records indicate that the species are allopatric.

As a precautionary measure, both palpi should be examined during determinations in this species group. Bilateral asymmetries and abnormal palpi will become apparent, and be less misleading.

Acknowledgments

I wish to thank Dr. R. Carter, Manitoba, and Mr. R. Huber, Minnesota, for collecting some of the specimens used in this study.

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BIONOMICS AND BEHAVIOR OF *ALLOXYSTA MEGOURAE*,
AN APHID HYPERPARASITOID
(HYMENOPTERA: ALLOXYSTIDAE)

Irene Matejko¹ and Daniel J. Sullivan, S. J.²

Abstract.—The authors studied *Alloxysta megourae* (Ashmead), a hyperparasitoid of the pea aphid, *Acyrtosiphon pisum* (Harris). Larval, prepupal, and pupal stages of the primary parasitoid (*Aphidius smithi*) found in non-mummified aphids are attacked by *A. megourae*. Several aspects of *A. megourae* development within its host differ from those described in other species of *Alloxysta*. The sensory structures on the tip of the ovipositor of *A. megourae* are described.

Introduction

Several hymenopteran families are aphid hyperparasitoids. These aphid hyperparasitoids can be divided into two categories based on their attack behavior. (1) *Endoparasitoids*: the female oviposits in the primary parasitoid larva and then the hyperparasitoid larva feeds internally. (2) *Ectoparasitoids*: the female oviposits on the surface of the primary parasitoid and then the hyperparasitoid larva feeds externally. We studied *Alloxysta megourae* (Ashmead), an endoparasitoid of *Aphidius smithi*.

The classification of *Alloxysta* was studied by Andrews (1978). Haviland (1921) was the first to comment on the relationship among three species of Alloxystidae (given as Cynipidae) and their primary parasitoid host. The embryology and larval development of *Alloxysta* (given as *Charips*) was described by Haviland (1921). Gutierrez and van den Bosch (1970a, b), Gutierrez (1970a-d), Sullivan and van den Bosch (1971) and Sullivan (1972) studied *Alloxysta (Charips) victrix* in the field and laboratory. The bionomics and behavior of *Alloxysta megourae* have not been reported before. The sensory apparatus on the ovipositor of *A. megourae* is described.

Materials and Methods

The pea aphid, *Acyrtosiphon pisum* (Harris), served as the host in this study, and was reared on broad bean, *Vicia fava* L. (Windsor variety).

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Table 1. Composite life cycles of the primary parasitoid, *Aphidius smithi*, and the hyperparasitoid, *Alloxysta megourae*, under laboratory conditions.

Age in days	<i>Aphidius smithi</i>	Age in days	<i>Alloxysta megourae</i>
0	Egg deposited in aphid		
1			
2	1st larval instar		
3			
4	2nd larval instar		
5			
6	3rd larval instar	0	Egg deposited in <i>Aphidius</i>
7		1	
8	Host aphid mummified ^a	2	Egg hatches (host aphid mummified)
9		3	
10	Prepupa (meconium voided)	4	1st larval instar
11	Pupa	5	
12	Adult emerges	6	2nd larval instar
		7	
		8	3rd larval instar
		9	
		10	Mature larva feeds externally
		11	
		12	Prepupa (meconium voided)
		13	Pupa
		14	
		15	
		16	
		17	
		18	
		19	Adult emerges

^a When hyperparasitized by *Alloxysta*, *Aphidius* ceases development.

Aphidius smithi Sharma & Subba Rao, the primary parasitoid, and *Alloxysta megourae* (Ashmead), the hyperparasitoid, were reared with the plants and aphids in a bioclimatic chamber (Percival Environator, Model E-54U) according to the method described by Bennett and Sullivan (1978).

The daytime (16 hr) temperature was $21.1 \pm 0.6^\circ\text{C}$ at $75 \pm 5\%$ RH. At night the temperature was $15.5 \pm 0.6^\circ\text{C}$ at $85 \pm 5\%$ RH.

The primary parasitoid, *Aphidius smithi*, was reared by placing 2–4 mated females in a glass tube with cut broad bean stems and 20 4th instar pea aphids. The tube was kept in the bioclimatic chamber for 6 hr. Then the wasps were removed and the parasitized aphids replaced on the broad bean leaves and returned to the temperature chamber. After 12 days, the adult *Aphidius* emerged from the aphids.

To observe the process of courtship and mating, the adult *Alloxysta* male and female were left undisturbed for 6 hr in the Dixie container. We ob-

served oviposition by placing 5–6 adult *Alloxysta* females in a 60 × 15 mm plastic Petri dish with 15 4th instar aphids. The life cycle of *A. megourae* (Table 1) was studied by a technique allowing continuous observation of all stages of development within the aphid mummy (Keller & Sullivan, 1976).

To determine whether *A. megourae* females attack both parasitized and unparasitized aphids, we placed a female *Alloxysta* in a Petri dish for 3 hr with a parasitized aphid having a 6–7-day-old *Aphidius* larva and an unparasitized aphid. All aphids used in 50 replicates were in the 4th instar. After the *Alloxysta* was removed, we dissected and recorded the eggs in each aphid.

Results and Discussion

Courtship and Mating

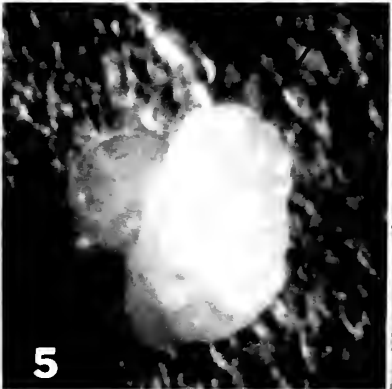
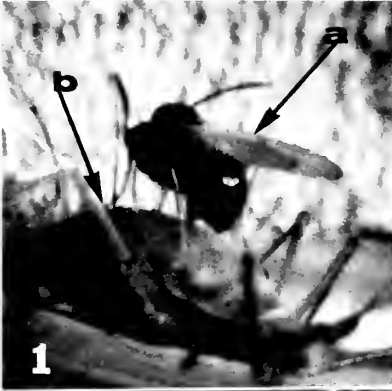
Alloxysta adults were able to mate soon after emergence. The courtship begins when the male follows the female around the observation chamber. His behavior was predictable: he positioned himself behind the female and tapped her abdomen with his antennae, while she remained motionless. This phase lasted from 2–7 minutes. More intensified courtship began when the male mounted the female. He climbed on her back with his legs firmly grasping the sides of her body. Pairs were frequently observed mounted, with the male on top of the female and being carried about by the female for as long 30 seconds to 1 minute. Copulation lasted from 10–20 seconds.

Oviposition Behavior

A. megourae behaves as an endoparasitoid. It attacks the *Aphidius* larva, which has been developing inside a live aphid, and deposits the egg within the primary parasitoid larva.

The egg-laying behavior of *A. megourae* has the following pattern: the female approaches the live parasitized aphid and rapidly antennates its surface. She then mounts the back of the aphid and assumes a squatting position with her abdomen slightly bent (Fig. 1). Once the *Alloxysta* female secures herself tightly on the dorsum of the aphid, the aphid moves violently as if trying to dislodge the wasp. She then inserts her ovipositor through the thin exoskeleton of the aphid and probes the aphid's hemocoel in search of the primary parasitoid larva (Fig. 2). If unsuccessful at that site, the *Alloxysta* female withdraws the ovipositor, moves to a new position on the aphid's dorsum and begins to probe again for the host. *A. megourae* females have not been seen to host-feed, neither before nor after oviposition nor do they paralyze their hosts.

It was not unusual to observe 4–5 *Alloxysta* females ovipositing at the same time on the same live, parasitized aphid. They were not easily dis-



turbed when ovipositing, even when some *Alloxysta* females climbed over and under each other while others were ovipositing. Once situated on the aphid, all 4 or 5 *Alloxysta* females probe simultaneously for the primary parasitoid within the aphid. Invariably, although several eggs may be laid, only one adult developed from each host. Once oviposition is completed, the *Alloxysta* female withdraws her ovipositor and abruptly leaves the aphid.

Sensory Structures on Ovipositor

Scanning electron micrographs of the sensory structures on the ovipositor of *A. megourae* are seen in Figs. 3 and 4. The ovipositor is composed of paired 1st valvulae, and a fused pair of ventral 2nd valvulae. Each of the 1st valvulae has three sensory pits. The 2nd valvulae have barbs on the outer surface, but no pits.

Development within the Mummy

Eclosion of the *Alloxysta* larva from the egg occurs about 72 hr after mummy formation and is encased within a white, opaque mass. The larva is translucent white with visible segmentation on the surface. It undergoes several instars, and as the larva increases in size, a color change is evident. It becomes bright yellow, almost indistinguishable from the yellow *Aphidius* larva.

By the 9th day after *Alloxysta* egg deposition, the surface of the *Aphidius* larva begins to change to a dark brown color, it appears wrinkled and slowly deteriorates. On the 10th day, the *Alloxysta* larva emerges from the *Aphidius* larva and begins to feed externally on it (Fig. 5). By the end of the 11th day, the entire *Aphidius* larva is consumed with the exception of the head capsule which is pushed to one side of the mummy. On the 12th day, the midgut and hindgut of *Alloxysta* are connected and the meconium is voided and is pushed against one side of the mummy. This begins the prepupal

Figs. 1-6. Ovipositional behavior and developmental stages of *Alloxysta megourae*. 1. Adult *Alloxysta* female exhibiting a typical drilling position (a) on the parasitized pea aphid (b). The head is down and the legs are firmly attached on the aphid's dorsum. (25 \times) 2. Adult female *Alloxysta* ovipositing with antennae extended straight back. (25 \times) 3. Scanning electron micrograph of the abdomen of an *Alloxysta* female with the ovipositor evident (a). (200 \times) 4. Scanning electron micrograph showing details of the structures located on the tip of an *Alloxysta* ovipositor. Three sensory pits (a) on the 1st valvulae and a row of barbs (b) on the fused 2nd valvulae are shown. (1000 \times) 5. A 10-day-old *Alloxysta* larva (a) emerging from its host, *Aphidius* (b), which it consumes within a few hours. (80 \times) 6. The characteristically irregular exit hole of *Alloxysta* located on the posteriodorsal side of the aphid mummy. (50 \times)

Table 2. Discrimination between parasitized and unparasitized aphids by the hyperparasitoid female *Alloxysta megourae* for oviposition (based on 50 replicates).

	Time in min. probing	Std. Dev.	No. of reinsertions	Std. Dev.	No. eggs laid	Std. Dev.
Parasitized	8.0	2.80	4.0	0.21	2.7	0.23
Unparasitized	5.6	2.71	3.4	0.25	0	0

stage which lasts about 24 hr. On the 13th day, the pupa is formed. It is bright yellow, but within 4–5 days, it gradually becomes dark brown. During this pupal stage, the hyperparasitoid was completely motionless. However, it did exhibit abrupt jerking movements if touched with a probe.

The adult *Alloxysta* emerges from the aphid mummy about 19 days after oviposition. The irregular-shaped emergence hole made by the *Alloxysta* adult was almost always located on the dorsal side of the aphid mummy (Fig. 6). Once emerged, the *Alloxysta* adult cleaned itself, fed on the honey-water mixture, and then began the courtship and mating behavior.

Discrimination between Parasitized and Unparasitized Aphids

The parasitoid attack behavior of *Charips* (*Alloxysta*) (Haviland 1921, Gutierrez and van den Bosch 1970b) is similar to that of *A. megourae*. However, Haviland (1921) reported that *Charips* selected only aphids containing a primary parasitoid whereas unparasitized aphids were ignored. Gutierrez (1970a) reported that *Charips victrix* (Westwood) probed unparasitized aphids. We found that *A. megourae* females always attacked and probed live aphids, both parasitized and unparasitized. These aphids were then dissected and in the 50 replicates, an average of 2.7 eggs were found in the *Aphidius* larvae, while no eggs were found in the unparasitized aphids (Table 2). Hence, discrimination appears to be accomplished during probing of the aphid with the ovipositor.

These data indicate several points: (1) *Alloxysta* females attacked unparasitized aphids but did not oviposit. (2) *Alloxysta* females attacked parasitized live aphids containing the *Aphidius* larva and would readily oviposit within the primary parasitoid host. However, the host larva may not always be detected since it may be in an inaccessible part of the aphid's hemocoel. In these situations, *A. megourae* changes position on the aphid's dorsum and probes and searches the hemocoel again (Gutierrez 1970a). Thus, not only does *Alloxysta* attack the same parasitized aphid more than once (Sullivan 1972) but a variable number of eggs are laid in the *Aphidius* larva within the aphid as a result of these attacks. A study of Table 2 would seem to indicate that there is no direct correlation between the number of ovipositional attempts and the actual number of eggs deposited.

Sensory Structures on Ovipositor

It has been known that sensory structures are important in host selection and host discrimination. Muesebeck and Dohanian (1927) stated that hyperparasitoids are less discriminatory than primary parasitoids in host selection. But, Gutierrez (1970d) showed that the ovipositor of *A. victrix* has sensory structures near the tip which apparently are used by this hyperparasitoid to discriminate among different species of primary parasitoid host larvae. In our study, *A. megourae* showed a similar morphology of the ovipositor. The 3 sensory pits are sensilla coeloconica as described by Snodgrass (1935) and Chapman (1969). However, in addition to Gutierrez' mention of the sensory pits on the paired 1st valvulae which probably have a chemosensory function, our photomicrographs also show 8 or more barbs on the outer surface of the 2nd valvulae. Probably these barbs anchor the 2nd valvulae during oviposition, while the 1st valvulae are inserted into the aphid's hemocoel in order to search for the *Aphidius* larva.

Acknowledgments

Special appreciation is expressed to Dr. F. G. Andrews (USDFA, Sacramento, California) for taxonomic determination of *Alloxysta megourae* (Ashmead).

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LARVA OF *CALOPTERON TERMINALE* (SAY) WITH ADDITIONAL
NOTES ON ADULT BEHAVIOR (COLEOPTERA: LYCIDAE)¹

Tim L. McCabe and Linnea M. Johnson

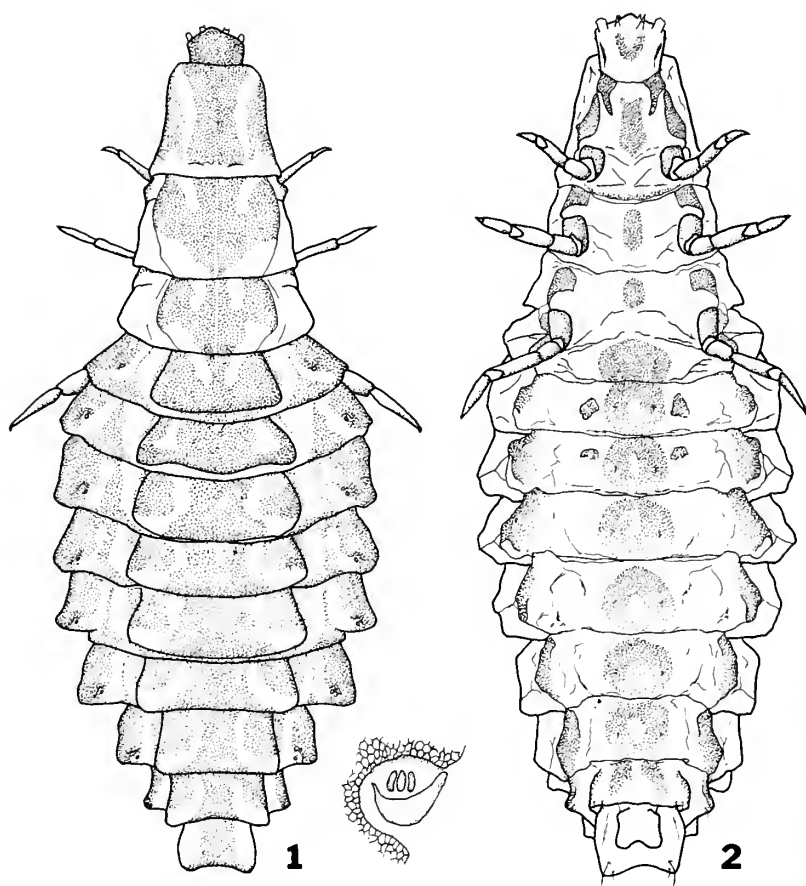
Abstract.—Gregarious behavior was observed in the pupae and adults of *Calopteron terminale* (Say) (Coleoptera: Lycidae). Predatory habits in the adults were not confirmed by experiments. The larva and pupa are described and illustrated.

Young & Fischer (1972) observed ultimate instar larvae of *Calopteron terminale* (Say) that were apparently seeking a pupation site. A description of the pupa and details on the pupation were given, based on captive specimens, although the larva was not described. The larval skin is not shed, but splits on the side and remains attached at the base similar to *Calopteron fasciatum* Fab. (Withycombe, 1926). According to Withycombe (1926): "When full grown, the larvae of *C. fasciatum* congregate in masses on the underside of the trunk for pupation. From a nucleus of early individuals a mass of several hundreds may radiate." Young & Fischer (1972) did not report gregarious pupation in *C. terminale*, but they were observing captive specimens. On August 15, 1971, mass pupation of *C. terminale* was observed near North Twin Lake, Becker County, Minnesota.

As with *C. fasciatum*, *C. terminale* would pupate in an expanding circle from a point of origin; this point being a hole in the bark from which the larvae were emerging. Thirty larvae and pupae were on the surface of the bark. The site was not revisited and more individuals may have emerged from beneath the bark. Several adults were observed eclosing at midday. Mating did not occur at the pupation site and unmated adults were observed taking their maiden flight. Mated pairs have been observed dropping from canopy aggregations of *C. terminale* in Minnesota and North Dakota and in canopy aggregations of *Lycus loripes* (Chevrolat) and *Lycus arizonensis* Green in Arizona. The weak flight of lycids is not capable of supporting two individuals and mated pairs frequently become dislodged and fall to the ground. Burke (1976) gave a detailed account of pre-copulatory behavior in *C. terminale*.

Eisner & Kafatos (1962) proved that the gregarious activities of *Lycus loripes* were facilitated by an unidentified pheromone emitted by the males.

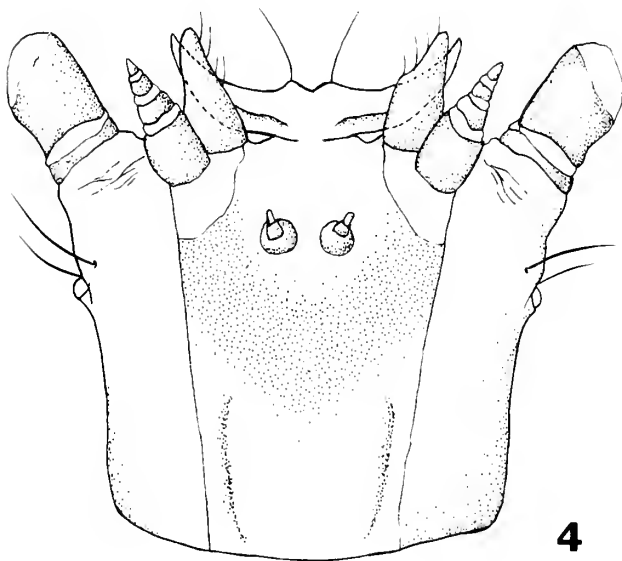
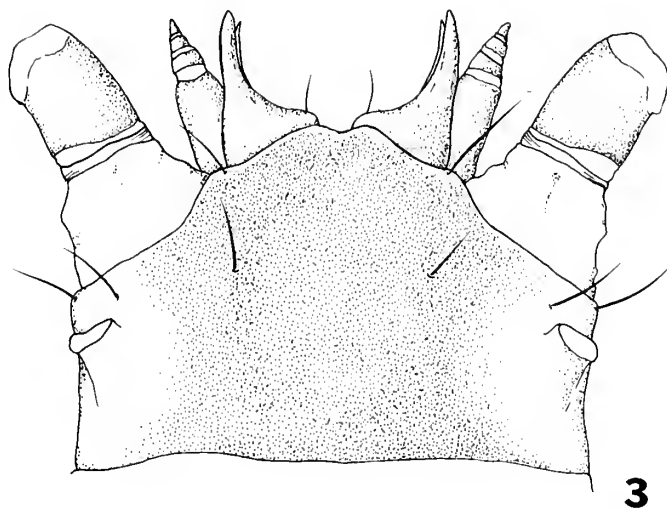
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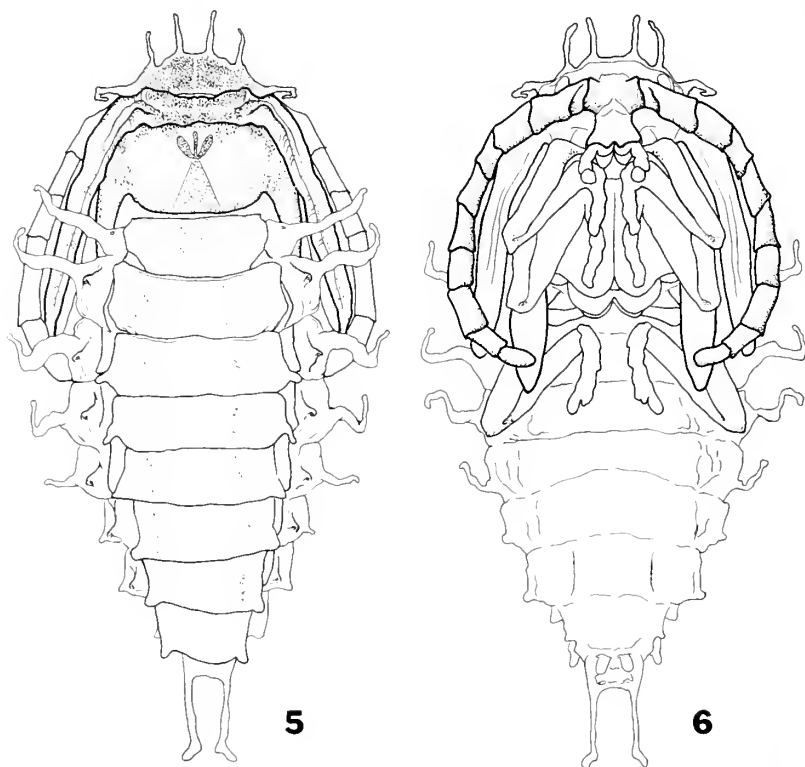
Figs. 1-2. *Calopteron terminale* (Say), mature larva, dorsal and ventral aspects (insert: abdominal spiracle). North Twin Lake, Becker County, Minnesota. Total length 14.0 mm.

It is not known if *C. terminale* employ a pheromone. The senior author and Robert Dregseth encountered an aggregation of several hundred *C. terminale* on June 22, 1972, near the Walcott Dunes, Richland County, North Dakota. The beetles were abundant in the uppermost leaves of a boxelder (*Acer negundo* L.). The tree was in a sunny location and was infested with aphids. A sample of the beetles was collected with an eight foot pole-and-net assembly from the roof of a van.

Young & Fischer (1972) and Britton (1967) speculated that the adults were predaceous. Four *C. terminale* adults from the Catskill Mountains, Greene County, New York, were deprived of food and water for three days. After this time, they were offered droplets of water upon which they drank until



Figs. 3-4. *Calopteron terminale* (Say), larval head capsule, dorsal and ventral aspects. North Twin Lake, Becker County, Minnesota.



Figs. 5-6. *Calopteron terminale* (Say), pupa, dorsal and ventral aspects. North Twin Lake, Becker County, Minnesota. Total length 12.7 mm.

satiated, then they were offered de-winged flies, chrysomelid larvae, mirid immatures, and a noctuid larva. They would not attack any of these and would actually make escape movements when one of the "prey" was encountered. Burke (1976) offered adults of *C. terminale* a small weevil larva, *Cossonus* sp., but could not get them to feed. The Catskill beetles were also offered aphids. Again, escape movements were noted when the prey were detected. Finally, honey dew from the aphids was provided. The beetles, even though satiated for water, fed readily on the honey dew. However, sugar solutions are readily taken in by beetles (Thorsteinson (1960); Gottschalk (1957)). Nonetheless, the presence of honey dew may be important for site selection in *C. terminale*. Linsley, et al. (1961) reported nectar and pollen feeding in *Lycus loripes*. In addition, *Lycus minutus* Green has been observed feeding on the staminate cones of *Salix* sp. in Miller Canyon, Huachuca Mountains, Arizona.

The pupa (Figs. 5 & 6) has been previously described by Young & Fischer

(1972) and a photograph of the pupa was reproduced. The dorsal tubercles found in the pupal stage are reminiscent of the larval tubercles of *Caenia dimidiata* Fab. (figured by Böving & Craighead, 1931) and suggests the close relationship of the two genera.

The larva of *C. terminale* lives beneath as well as upon the bark of dead trees, apparently showing a preference to erect trunks. Lycid beetle larvae of the tribe Lygistopterini also occur under bark or in rotten wood, but many Lycini larvae can be taken on open ground at night. Larvae of *C. terminale* are probably lignivorous as is *C. fasciatum* (Withycombe, 1926). The description is based on an ultimate instar larva.

The Larva of *Calopteron terminale* (Say)

General.—Onisciform; 14 mm long, 5 mm wide; body depressed, curved in lateral view, with dark brown markings on a brown body, glabrous.

Head.—Prognathous, depressed, subquadrate, partially hidden by prothorax; frontal and epicranial sutures absent; frons, clypeus, and labrum fused; a single large ocellus on lateral margin posterior to each antenna; antennae prominent, two-segmented, basal segment a narrow ring, terminal segment short, blunt, "dome shaped," with membranous tip; mandibles falciform, each bearing single, short seta, in two parts, inner ensheathed by outer shell, curved at tip, opposed at base; maxillary palpi conical, each 4-segmented; galea subequal to palpus in length, bearing 4 short setae; stipes and cardo fused to enlarged mentum; labial palpi small, one-third length of maxillary palpi, 2-segmented, each arising from membranous basal segment, approximate to each other but distant from base of maxillary palpus; mentum and submentum fused.

Thorax.—Prothorax longest of three sequentially decreasing segments; prothoracic spiracle located near anterior margin of mesothorax within lateral sclerotized projection; meso- and metathorax with somewhat circular dorsal shield; legs moderately long, tibia bearing tiny hairs, tapering to single tarsal claw.

Abdomen.—Depressed, widest and thickest at mid-abdominal region, segments 1–8 with elevated subquadrate dorsal shields, distinct lateral flanges sclerotized dorsally; abdominal spiracles (Fig. 1) apparently of an annular biforous type with annular portion inconspicuous, borne on tubercle; ventral abdominal aspects with circular markings each bearing two extremely minute setae; segment 9 flat, posterior margin concave bearing 4 short setae ventrally; urogomphi absent.

Material examined.—One mature larva, North Twin Lake, Becker County Minnesota, August 15, 1971, collected and determined by association with reared adults by T. L. McCabe.

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NOTES ON A POPULATION OUTBREAK OF THE BEETLE
UROPLATA SP. (COLEOPTERA: CHRYSOMELIDAE)
ON THE TREE *BUNCHOSIA PILOSA*
(MALPIGHIACEAE) IN COSTA RICA

Allen M. Young

Abstract.—An outbreak of the herbivorous beetle *Uroplata* sp. (Chrysomelidae) on the tree *Bunchosia pilosa* H.B.K. (Malpighiaceae) in the central highlands of Costa Rica is described. During the early phase (June) of the rainy season, adult beetles were abundant on leaves of lower branches, where they feed by stripping away tissue from the upper side of leaves. Immature stages of the beetle were not seen, nor was any mating activity observed during the morning hours. Beetles do not feed on the very pilose undersides of the leaves. No other herbivores were seen. As the rainy season advances, the *Uroplata* infestation spreads into the upper portions of the tree, perhaps as a response to increasing adult density and depletion of food supply in the lower region. Infestations were large during June and July (1974) but diminished by August. The phenomenon of population outbreaks in tropical herbivorous insects is discussed.

In the American tropics, the traditional view of insect-plant interactions in relation to community structure has been one of biotically-controlled herbivore populations seldom attaining population outbreak conditions (Pianka 1966). Therefore, population outbreaks of herbivorous insects should be documented and follow-up experimental studies conducted whenever possible.

The purpose of this paper is to call attention to a population outbreak of the beetle *Uroplata* sp.* (Coleoptera: Chrysomelidae) on the tree *Bunchosia pilosa* H.B.K. (Malpighiaceae) in the central highlands of Costa Rica. Owing primarily to the highly specialized and coevolved feeding relationships between herbivorous insects and their host plants in the tropics (Janzen 1973) and the apparent maintenance of rather stable insect populations that fluctuate primarily with seasons in the tropics (e.g., Janzen and Schoener, 1968; Wolda, 1978a, b), the frequency of outbreaks of herbivores associated with any one host plant species is expected to be low. The documentation of such outbreaks in the tropics provides information that can be used for further studies on the regulation, or lack thereof, of insect populations in

* The taxonomy of Neotropical *Uroplata* is presently too unclear to assign a correct specific name to the species studied in this paper.

the tropics. This paper describes some of the major features of the *Bunchosia-Uroplata* interaction. I use the term "outbreak" in this paper to refer to a large population increase of a phytophagous insect species on a single individual of a tree species. In the traditional sense, outbreak refers to large numbers of insects on many plants in an area. In the tropics, given the very patchy spatial distribution of many tree species, outbreaks may be confined to only certain individuals of a certain species.

Locality and Study Methods

The interaction of *Uroplata* beetles with *Bunchosia* was studied June–August 1974 at "San Rafael de Ojo de Agua" (1,000 m elev.), Alajuela Province, Costa Rica, a region described as "tropical moist forest" (Holdridge, 1967). The study site was a single individual adult *Bunchosia* tree (about 10 m tall) growing along the Rio Segundo. At this locality the river is lined predominantly with *Zygia longifolia* (H.&B.) Britton & Rose (Leguminosae) trees. The single *Bunchosia* was the only one of this species encountered in a 0.25 km river-edge survey (both sides) and no individuals were found in nearby pastures (back to 500 m from either side of the river). On June 26, at least several hundred adults of *Uroplata* were discovered on this tree during a census of emerging adult cicadas (Young, 1979). The flattened, almost rectangular black beetles (10 mm long) were easy to see on the leaves. This locality is highly seasonal in terms of the annual monthly pattern of rainfall; a distinct dry season, with little or no rain, occurs between January and April and therefore the observations on *Uroplata* were made in the early rainy season.

Observations were made on the *Bunchosia-Uroplata* interaction over a three-day period in June. The following types of information were recorded: (1) description of damaged parts of the tree, (2) presence of beetles on other trees within 40 m to either side of the infested *Bunchosia* tree, (3) vertical distribution of the infestation on the tree including an examination for immature stages, (4) intensity of the infestation in shady versus sunlight portions of the tree, (5) density of the beetles in sections of high and low infestation, and (6) percentages of leaves destroyed by the beetles on branches of high and low infestation. In addition, the infestation was examined during July and August. The presence of other feeding insects on the *Bunchosia* tree was also noted.

To measure the intensity and vertical pattern of leaf damage from *Uroplata*, several branches were selected from both lower and upper portions of the tree; lower branches were those below 3 meters from the ground. The number of both healthy and damaged leaves on each of several branches from the two regions was recorded as was the number of feeding beetles per leaf. In areas of high and low infestation, an area 2 meters long by 1.5



Fig. 1. A branch of *Bunchosia pilosa* showing leaves damaged by feeding *Uroplata* beetles. The light areas on the leaves are where the beetles have destroyed leaf tissue.

meters high was used to count the number of beetles present and feeding. As estimate of the vertical distribution of the infestation was made by counting the number of light brown patches from top to bottom of the tree. Owing to the large size of the leaves (120 cm²) and the conspicuousness of the brown patches against the dark green color of healthy tissue, it was easy to estimate the distribution of attack by counting damaged leaves with the naked eye and binoculars.

Results

Uroplata beetles were found only on the *Bunchosia* tree and not on other trees and herbaceous plants in the area. Only adult beetles were found on the tree and these fed in small groups (5–40 beetles) in neat rows. Adults scraped away tissue from the smooth upper side of a leaf. No beetles were seen feeding from the very pilose undersides. The result of this feeding behavior was that leaves damaged by the beetles had large areas of light brown dead tissue (Fig. 1) as beetles did not chew all the way through the

Table 1. Some summary statistics describing the infestation by *Uroplata* beetles as herbivores of the tree *Bunchosia pilosa*.

(1) Branch position (and leaves) and pattern of leaf destruction for 10 lower and 8 upper branches

	Mean no. leaves per branch ($\bar{x} \pm \text{S.D.}$)	Mean no. leaves with >33% destroyed surface ($\bar{x} \pm \text{S.D.}$)	Mean % damage (\bar{x})
Lower	48.3 \pm 22.7	20.9 \pm 10.2	44.7 \pm 9.62
Upper	45.9 \pm 26.3	8.4 \pm 8.1	12.9 \pm 11.7

(2) Beetle density and approx. % destruction of leaves in 2 patches of high infestation

	Mean no. beetles per leaf ($\bar{x} \pm \text{S.D.}$)	Mean % leaves destroyed, and range
Patch no. 1 (12 leaves)	8.3 \pm 11.1	57.5 \pm 24.7
Patch no. 2 (12 leaves)	9.3 \pm 4.5	50.0 \pm 10.0

(3) Beetle density and approx. % destruction of leaves in 2 patches of low infestation

	Mean no. beetles per leaf ($\bar{x} \pm \text{S.D.}$)	Mean % leaves destroyed, and range
Patch no. 1 (10 leaves)	0.6 \pm 1.5	4.0 \pm 4.6
Patch no. 2 (15 leaves)	1.5 \pm 2.3	1.3 \pm 2.9

leaves. Feeding beetles were found during both morning and afternoon hours. Nocturnal feeding was not determined.

Using 33% of more destroyed leaf surface as an indicator of "intense herbivore damage" in this system, leaves on the lower branches were found to be more damaged than leaves on upper branches (Table 1). Leaves of the lower branches had many large brown spots (Fig. 2). In two different patches of intense feeding, the *Uroplata* density was between 8 and 9 beetles per leaf, and with 50% or more of the leaves destroyed (33% or more damage of leaf surface area) in the two samples (Table 1). In sharp contrast, in two patches of low predation, there was about one beetle per leaf (0-2 beetles) and less than 5% of the leaves were severely damaged (Table 1). The leaves of lower branches were more severely damaged than leaves on upper branches (Table 2). On lower branches in patches of intense predation, the actual range in percentage of surface area destroyed per leaf was 30% to 90% even though beetle abundance per leaf was more variable (Table 3). No other insects were observed feeding on the leaves and no immature stages of *Uroplata* were present. No copulating pairs of beetles were seen.

The greatest numbers of beetles were found on leaves in the shade. When a branch bearing leaves being attacked by the beetles was pulled into the



Fig. 2. The lower branches of this *Bunchosia pilosa* tree had many leaves severely damaged by *Uroplata* beetles during the rainy season.

direct sunlight, beetles crawled away within 2–8 minutes. During the morning hours, the beetles occurred in greatest numbers on the upper sides of leaves, and by 1:00 P.M. on sunny days, most beetles moved to the ventral sides of the leaves. Large aggregations (8–40 beetles) were found resting on the undersides of partially or completely destroyed (brown) leaves in the afternoon.

Although the *Uroplata* infestation was high during June (June 26–28), the infestation was even greater on July 14 and 30 and at this time it had spread to the upper portion of the tree. By August 11 no beetles were present on the tree.

Although, as reported above, the infestation of adult beetles on the tree was very large during the 1974 wet season, no outbreaks were seen on this tree over several other years, namely from 1971–1973 and again in 1975. The study site was visited several times in both wet and dry seasons in these years, and no outbreaks of *Uroplata* were seen. There were no outbreaks in three successive years preceding the outbreak year, or in the year following it. Furthermore, the appearance of outbreak numbers of adult

Table 2. The distribution of the infestation of *Uroplata* beetles (Chrysomelidae) on a mature individual of the tree *Bunchosia pilosa* (Malpighiaceae) in central Costa Rica.

Branch positions	Branch no.	No. leaves per branch	No. leaves 33% destroyed	% Destroyed
"Low"*	1	19	8	42%
	2	36	20	56%
	3	27	14	52%
	4	77	35	45%
	5	83	42	51%
	6	41	15	36%
	7	43	19	44%
	8	64	19	30%
	9	26	15	58%
	10	67	22	33%
"High"	1	94	21	22%
	2	72	15	21%
	3	55	17	31%
	4	41	7	17%
	5	35	4	11%
	6	30	1	0.3%
	7	23	1	0.4%
	8	17	1	0.6%

* "Low" branches are those 3 meters or less above the ground; "high" branches are above 3 meters to top of canopy.

beetles on the tree was seen only in the 1974 wet season, despite the fact that a distinct dry season occurs in the region.

Discussion

From studying herbivorous insects in the Central American tropics over the past 11 years, I attach the term "population outbreak" to the infestation of *Uroplata* beetles on *Bunchosia* since the numbers found were far greater than I have seen for Chrysomelidae on many plant species, and generally for other herbivorous insects in general. For the Chrysomelidae, in herbaceous to slightly woody plants with a canopy of 2 meters or less (in secondary succession), beetle numbers per plant generally ranged from 1-20 (pers. obs.). During the early rainy season in Costa Rica, new flushes of vegetative growth on many plant species promotes the growth of insect populations (Janzen and Schoener, 1968; Janzen, 1973) and herbivorous insects may synchronize emergence and peak adult abundance with periods of high availability of plant tissue utilized as food.

In natural communities, predators and parasites on herbivorous insect species are also expected to have population cycles synchronized with their hosts (Allee et al., 1949). In plant communities where human or catastrophic

Table 3. The distribution of *Uroplata* beetles in two patches* of lower branches of the tree *Bunchosia pilosa* where infestations were high.**

<i>Bunchosia</i> leaf patch	Leaf code no.	No. beetles present	% Leaf area destroyed
1	1	3	90%
	2	39	75%
	3	3	90%
	4	0	30%
	5	9	30%
	6	0	40%
	7	20	75%
	8	2	20%
	9	6	45%
	10	6	45%
	11	9	50%
	12	2	90%
2	1	11	60%
	2	9	50%
	3	3	40%
	4	4	60%
	5	4	50%
	6	12	50%
	7	11	70%
	8	7	40%
	9	8	30%
	10	8	50%
	11	12	50%
	12	9	60%
	13	7	40%
	14	14	50%
	15	21	50%

* Each "patch" has a one-by-one meter area of dense leaves within the lower branch region of the tree.

** The areas of high beetle densities were selected in the lower branch region at the time of census. Censuses in both patches were conducted between 9:50 A.M. and 1:00 P.M. on the same day, with about equal time spent counting beetles and leaf damage in each one.

disturbance has resulted in a reduction of plant species diversity locally, the probability of outbreaks of herbivorous insects is greater than in communities characterized by higher plant diversity (Pimentel, 1961). Climatic explanations of insect outbreaks are generally confined to regions characterized by harsh environmental conditions with large fluctuations annually (Elton 1927). Such effects are generally not expected in the tropics, although the interaction of (1) highly synchronized population cycles in seasonal environments and (2) the long-term reduction in host plant diversity are expected to result in population outbreaks of herbivorous insects in the trop-

ics. Is this what is occurring the the *Bunchosia-Uroplata* system in central Costa Rica in the early rainy season? With more data from several trees, I believe that the answer to this question would be "yes."

Regions of the world with considerable variations in annual rainfall promote large fluctuations in insect abundance (Birch, 1957; Wolda, 1978b). The central highlands of Costa Rica represent seasonal environments in terms of rainfall, and year-to-year variations in rainfall may contribute to fluctuations in insect populations, perhaps in some years pushing some species into the population abundance zone of outbreak conditions. Consistent and comparable annual rainfall data for San Rafael de Ojo de Agua are not available for such a correlation for the *Bunchosia-Uroplata* interaction. Sixty genera and approximately 800 species of woody vines, shrubs and trees comprise the Neotropical Malpighiaceae, and *Bunchosia* is one of the largest genera (Hartshorn 1971). *Bunchosia pilosa*, known in Costa Rica as "Cerezo" or "Orquetilla," occurs most commonly between 110–1,800 meters above sea level and ranging from Costa Rica to Colombia (Standley 1937). Hartshorn (1971) mentions that *B. pilosa* is rare at "Finca La Selva" in the northeastern lowland rain forest (98 m elev.) region of Costa Rica. This tree generally has a patchy spatial distribution in highland forest environments and as such, it is probably a highly dispersed and inconspicuous resource for host-specific herbivores. Furthermore, in the central highlands of Costa Rica, a large percentage of natural forest has been removed as the result of human activity, contributing to the scarcity of this tree at localities such as San Rafael de Ojo de Agua. At this locality, forest trees are presently limited to the margins of rivers and streams, sometimes in steep gulleys. If this particular species of *Uroplata* is host-specific for *Bunchosia*, infestations of this herbivore will also be patchy. In highly disturbed habitats, the interactions between *Buchosia* and *Uroplata* could result in outbreaks of the beetle if reduction in plant species diversity has also resulted in a reduction in the availability of predators and parasites of the beetle (see Pimentel, 1961 for a general discussion).

The data suggest that the *Uroplata* infestation begins and mushrooms in the lower region of the *Bunchosia* tree. The spread of the infestation into upper portions of the tree later could be a density-related response to increased adult densities and decreasing food supply in the lower region during the rapid growth of the adult beetle population.

Although the outbreak numbers of adult beetles occurred during the early phase of the 1974 wet season, a large larval population must have been present prior to this period. The life cycle of *Uroplata* beetles is not known, and as pointed out by Arnett (1963), most of the species in the tribe Uroplatini of the subfamily Hispinae (about 1,500 species world-wide) are tropical and very poorly described and far less understood. Whether or not there is an actively growing larval population in the dry season, or whether the

dry season is passed as a diapausing egg, larva, or pupa, remains to be studied. In some species of phytophagous beetles, adult numbers are regulated by interspecific competition, and sometimes the intensity of such competition is influenced by local climatic factors (Utida, 1961). Populations of a host-specific temperate-zone weevil *Sitona regensteiniensis* are regulated by heavy mortality of eggs and larvae from parasites and predators (Danthanarayana, 1969). It is sometimes the case that both density-dependent and density-independent factors regulate populations of phytophagous beetles (Parnell, 1966; Beaver, 1967). Part of the explanation of outbreaks of locusts is related to annual variations in rainfall patterns in target areas (Gunn and Symmons, 1959). A sudden outbreak of *Uroplata* beetles on *Bunchosia* could result from very favorable climatic conditions affecting larval populations. Furthermore, given the highly disturbed condition of the habitat, predators and parasites of *Uroplata* may no longer be present, reducing the operation of density-dependent mortality factors and increasing the role of density-independent factors such as rainfall or lack thereof. In the Chrysomelidae, the larvae often feed on the same host plants as the adults (Huffaker, 1953) and can sometimes become severe defoliators when regulatory factors are absent. Given the high densities of *Uroplata* adults, and although the sample is small, larval survival must have been very high, suggesting an absence of density dependent control or unfavorable climatic conditions in this particular year. As the outbreak was not present in other years, variations in climatic conditions may affect predators and parasites of *Uroplata* on this tree.

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FIELD STUDIES AND PARASITES OF *LIRIOMYZA*
TRIFOLIEARUM (DIPTERA: AGROMYZIDAE) IN
NORTHEASTERN USA

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Abstract.—*Liriomyza trifoliarum* Spencer, a native serpentine leafminer of alfalfa in the USA and Canada exists at low population densities. In 1978 the density averaged 0.2 mines per stem with a maximum of 1.3 mines per stem. It is controlled biologically (63% parasitism over a 4-year period) by 17 native parasite species plus 2 from Europe that recently were established against *Agromyza frontella* (Rondani). A list is provided of recovered parasite species and numbers of hosts parasitized by each species.

Liriomyza trifoliarum Spencer, a native serpentine leafminer that is not of economic importance, has been reported from Florida, California, and Prince Edward Island, Canada (Spencer, 1973). We found it on alfalfa throughout the northeastern USA and in Ontario, Canada; thus, its distribution is probably Nearctic on alfalfa. It also has been recovered from *Pisum sativum* L., *Trifolium incarnatum* L., and *T. repens* L. (Spencer, 1973). The present study was conducted in Delaware, south-central New Jersey, and southeastern Pennsylvania, coincidentally with studies of the alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani), an imported European pest of alfalfa. The purpose of our study was to present basic observations on field populations of *L. trifoliarum* on alfalfa and compile a list of species of recovered parasites with numbers of parasitized hosts. The order, family, and identifier of species mentioned in this paper appear in Table 1.

In studying *L. trifoliarum*, we had difficulty separating its larvae or puparia from those of other agromyzid species infesting alfalfa: ABL, *L. trifolii*, and the vegetable leafminer, *L. sativae*. (*Liriomyza sativae* was never collected by us in the northeastern USA, but it was reported from Ohio (Spencer, 1973) and from greenhouses in Canada (McClanahan, 1978), from which it might escape.) We made no effort to separate these species by larval morphology, since many larvae were completely consumed by developing parasites. Agromyzid species were distinguished by mine type, frass distribution, and pupation habit (Table 2).

In both field and laboratory studies, we observed that *L. trifoliarum* always pupated in the leaflet. When isolated leaflets containing puparia were placed in tight-fitting petri dishes, the epidermis of the drying leaflet occasionally ruptured, and the puparium dropped out after formation. This is

Table 1. Order, family, and identifier of species mentioned in this paper.

Species	Species
HYMENOPTERA: BRACONIDAE	HYMENOPTERA: PTEROMALIDAE
<i>Dacnusa dryas</i> (Nixon) ^a	<i>Bubekia fallax</i> Gahan ^b
<i>Opius dimidiatus</i> (Ashmead) ^a	<i>Halticoptera circulus</i> (Walker) ^e
	<i>Halticoptera laevigata</i> Thomson ^e
HYMENOPTERA: EULOPHIDAE	DIPTERA: AGROMYZIDAE
<i>Achrysocharella formosa</i> (Westwood) ^c	<i>Agromyza frontella</i> (Rondani) ^d
<i>Chrysocharis clarkae</i> Yoshimoto ^e	<i>Liriomyza sativae</i> Blanchard ^d
<i>Chrysocharis giraulti</i> Yoshimoto ^e	<i>Liriomyza trifoliarum</i> Spencer ^d
<i>Chrysocharis pubicornis</i> (Zetterstedt) ^e	<i>Liriomyza trifolii</i> (Burgess) ^d
<i>Chrysocharis punctifacies</i> Delucchi ^e	
<i>Closterocerus cinctipennis</i> Ashmead ^b	
<i>Closterocerus tricornatus</i> (Ashmead) ^b	
<i>Diauliniopsis callichroma</i> Crawford ^f	
<i>Diglyplus intermedius</i> (Girault) ^b	
<i>Diglyplus pulchripes</i> (Crawford) ^b	
<i>Diglyplus websteri</i> (Crawford) ^f	
<i>Pediobius bucculatricis</i> (Gahan) ^b	
<i>Pnigalio minio</i> (Walker) ^c	
<i>Zagrammosoma multilineatum</i> (Ashmead) ^b	

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^f R. M. Hendrickson, Jr.

perhaps what Spencer (1973, p. 99) referred to when he said, "Pupation appears to be variable, either in or outside the mine."

During 3 seasons (1975-77), we collected mined leaflets and recovered parasites at 7 fields (1 at Newark, DE; 3 near Oxford, PA; and 3 near Rancocas, NJ) by the method of Hendrickson and Barth (1979). The same procedure was followed in 1978 except the collection of 50 mined leaflets from each field was limited to *Liriomyza* spp. only, which were separated to species at the laboratory. In 1978, we also collected 20 alfalfa stems from each field and kept them fresh in a plastic bag in a car refrigerator. At the laboratory, the mines of ABL, *L. trifoliarum*, and *L. trifolii* were counted, disregarding the condition of the mining larvae. The ratio of mines of ABL:*L. trifoliarum*:*L. trifolii* was ca. 1800:40:1. *Liriomyza trifolii* was first found in mid-July 1978, on late 2nd-cutting alfalfa, and thereafter infrequently through October. It was probably present before July, but we did not encounter it, perhaps because the density was extremely low.

The average season-long density of *L. trifoliarum* was 0.2 mines/stem; maximum density was 1.3 mines/stem. If a leaflet was mined, we usually

Table 2. Some characteristics for distinguishing species of Agromyzidae found on alfalfa in northeastern USA.

Species	Mine type	Frass distribution	Pupation site
<i>Agromyza frontella</i>			
1st and 2nd instars	linear	broad strips	
3rd instar	blotch	broad strips	soil
<i>Liriomyza trifoliarum</i>	serpentine	isolated lumps	leaflet
<i>Liriomyza trifolii</i>	serpentine	narrow strips	soil
<i>Liriomyza sativae</i> ^a	serpentine	narrow strips	soil

^a A species which was potentially collectible, but that we never found in this area.

found 1 mine/leaflet; the maximum was 4 mines/leaflet. We found *L. trifoliarum* first in late May ca. 7–10 days after the first appearance of ABL mines and often in the same leaflet as ABL larvae. This was not surprising, since ABL larvae may mine >50% of the leaflets in a field at peak infestations.

Liriomyza trifoliarum makes feeding perforations through either the upper or lower leaflet epidermis. These perforations are angled rather than perpendicular, and do not penetrate to the opposite epidermis. When viewed against the sky, they appear light green. In contrast, ABL feeding perforations are always made through the lower leaflet epidermis, are perpendicular, and penetrate to or through the upper leaflet epidermis, giving the impression of clear "pinholes" when viewed against the sky.

Liriomyza trifoliarum pupates in the alfalfa leaflet. Thus at each harvest, some puparia are removed from the field. However, we think that most of the puparia remain in the field on the soil in dehiscent leaflets. Nearly all leaflets have dropped from the lower half of stems by harvest because of senescence. Any puparia in these leaflets are on the soil. Some puparia in leaflets on the upper half of the stem are also on the soil, according to our observation that leaflets mined by agromyzids dehisce before adjacent undamaged leaflets. This inclination is exacerbated during rainy weather, when moisture accelerates development of secondary plant pathogens in mines, and rain and wind cause mechanical dehiscence.

Parasitism of *L. trifoliarum* in 1978 was: 1st cutting, 28% (131 live forms); 2nd cutting, 38% (373 live forms); 3rd cutting, 74% (188 live forms); and post-3rd cutting, 79% (577 live forms). (Live forms are leafminer larvae or puparia that produce either adult *L. trifoliarum* or parasites.) For the 4 sampling periods, parasitism averaged 55% and totaled 62% (1,269 live forms). For the 4 seasons (1975–78), total parasitism was 63% (2,291 live forms); the parasite species and numbers of parasitized hosts appear in Table 3. To our knowledge, these were all primary parasites.

Table 3. Parasite species and numbers reared from *Liriomyza trifoliarum* collected in Delaware, southern New Jersey, and southeastern Pennsylvania, 1975-78.

Species	Recovered from		Number of hosts ^a
	Larva	Pupa	
<i>Diglyphus intermedius</i>	×		372
<i>Opius dimidiatus</i>		×	266
<i>Chrysocharis clarkae</i>	×	×	202
<i>Chrysocharis giraulti</i>	×	×	183
<i>Diglyphus pulchripes</i>	×		91
<i>Halticoptera circulus</i>		×	40
<i>Halticoptera laevigata</i>		×	30
<i>Pnigalio minio</i>	×		30
<i>Closterocerus tricinctus</i>	×		28
<i>Diaulinopsis callichroma</i>	×		28
<i>Achrysocharella formosa</i>	×		22
<i>Closterocerus cinctipennis</i>	×		21
<i>Diglyphus websteri</i>	×		14
<i>Pebibius bucculatricis</i>		×	6
<i>Chrysocharis punctifacies</i> ^b		×	4
<i>Dacnusa dryas</i> ^b		×	3
<i>Bubekia fallax</i>		×	2
<i>Chrysocharis pubicornis</i>		×	2
<i>Zagrammosoma multilineatum</i>	×		1
Unidentifiable ^c			94
		Total	1,439

^a Occasionally more than 1 parasite emerged from a host.

^b Introduced European species released against *Agromyza frontella*.

^c Adults were damaged or lost, or larvae were in diapause.

The European parasites *Dacnusa dryas* and *Chrysocharis punctifacies*, established in 1978 against ABL in Delaware (Hendrickson, 1978), were both recovered from *L. trifoliarum* in 1978. Thus this serpentine leafminer, found throughout the range of ABL, may serve as an effective alternate host in the biological control of ABL.

Although we never observed predation, we found indirect evidence of it. One or more small, round punctures through the leaflet epidermis over the integumental remains of *L. trifoliarum* larvae suggested that one or more of the hemipteran predators that are found on alfalfa had fed on the larvae. These punctures were distinctly different from feeding perforations made by adult female agromyzids.

Hendrickson and Barth (1979) reported that 12 of the 14 species of native parasites that attack ABL were derived from native *Liriomyza* spp. on alfalfa. These 12 species were all recovered from *L. trifoliarum*, and some were recovered from *L. trifolii*. In 1978, we recovered a single individual of a 13th species, *Zagrammosoma multilineatum*, from *L. trifoliarum*. The

finding that in 1978 the larval population of *L. trifoliarum* was ca. 40 times that of *L. trifolii* indicated that the native parasite complex that attacked ABL was derived almost entirely from the parasites of *L. trifoliarum*.

Our data indicated that *L. trifoliarum* is not of economic importance on alfalfa in the northeastern USA and Canada because it is kept at low population densities by 19 species of parasites and one or more species of predator.

Acknowledgment

This research was conducted with the technical assistance of Susan E. Barth.

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THREE NEW MIDDLE AMERICAN SPECIES OF AQUATIC
BEETLES IN THE GENUS *NOTIONOTUS* SPANGLER
(HYDROPHILIDAE: HYDROBIINAE)

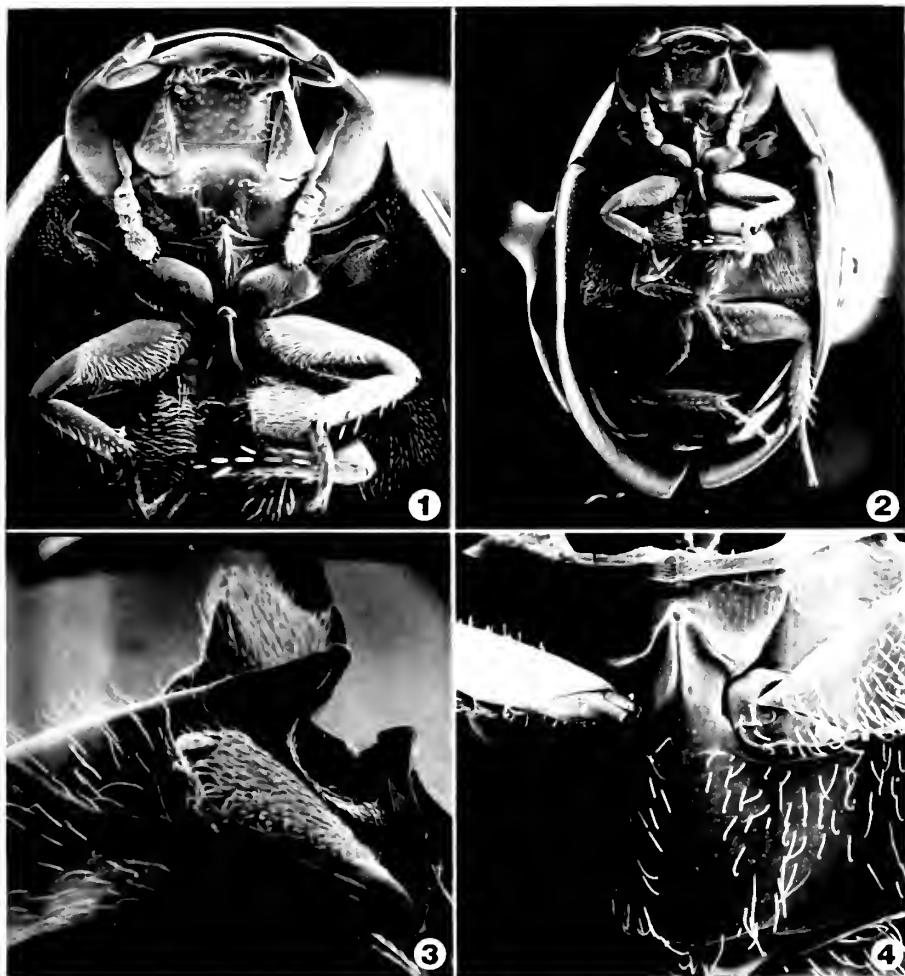
Philip D. Perkins

Abstract.—Three new species of the aquatic beetle genus *Notionotus* Spangler (Hydrophilidae) are described, one each from Mexico, Guatemala and Panama. Shared characteristics of these species which differ from those of the two previously described species from Venezuela are discussed and illustrated with scanning electron micrographs. Aedeagi of the new species, *N. mexicanus*, *N. nucleus* and *N. tricarinatus* are illustrated. Habitat preferences of *N. mexicanus* and *N. nucleus* are discussed, illustrated and contrasted with those of Venezuelan species.

Introduction

The aquatic beetle genus *Notionotus* was erected by Spangler (1972) for two species of Hydrophilidae from Venezuela. Described herein are three new species of *Notionotus* from Middle America, including one species each from Mexico, Guatemala and Panama. Based upon external similarities, these Middle American species form a monophyletic group and constitute the first known members of a lineage which possibly has a sister-group relationship with the Venezuelan species. The three Middle American species have the mesosternum longitudinally carinate in the midline, whereas in the Venezuelan species the median region is flat (cf. Figures 1, 4). The hind femur of Middle American species is more extensively pubescent, having only the apical $\frac{1}{4}$ lacking pubescence, whereas the hind femur of Venezuelan species lacks hydrofuge pubescence in the lower $\frac{1}{2}$ of the midregion as well as apically (Figure 2; see also figure 6 in Spangler, 1972). The front femur of all 5 species lacks hydrofuge pubescence on the upper surface basally, although this region is alutaceous in some (Figure 2, cf. figure 4 in Spangler, 1972). Additionally, the known Middle American species have testaceous elytra in contrast to the Venezuelan species which are either banded basally with reddish brown (*rosalesi* Spangler) or completely piceus (*liparus* Spangler).

There also appears to be differences in habitat preferences of the two putative sister-groups. Spangler (1972) collected the Venezuelan species in macicolous habitats such as "on the wet surfaces of rocks, in crevices, and on leaves in spring seepage areas in road cuts." However, *Notionotus* that my wife Maureen and I collected in Mexico and Guatemala were not found



Figs. 1-4. 1, *Notionotus liparus* Spangler, ventral aspect ($\times 10$); 2, as above ($\times 55$); 3, *N. nucleus* new species, lateral aspect of meso- and metathorax ($\times 230$); 4, as above, ventral aspect ($\times 195$).

in madicolous habitats. Specimens of *mexicanus*, new species, were collected from plant debris which had become trapped between stones in a rapid stream (Figure 8); specimens of *nucleus*, new species, were collected by stirring small stones, gravel and plant debris at the margin of a very small, slowly moving brook in dense vegetation, allowing the disturbed material to drift into an aquatic net, and carefully sorting the contents. My suspicions that *Notionotus* species from Middle America are not strictly

hygropetric are reinforced by the fact that my wife and I collected many specimens of the strictly madicolous hydrophilid *Oocylus* in several localities in Guatemala and Mexico, but were unable to find a single specimen of *Notionotus* in such habitats.

Key to Species of *Notionotus*

1. Mesosternal process flat or weakly rounded (Figs. 1, 2); pubescence of hind femur less developed, absent from lower $\frac{1}{2}$ of midregion as well as apically (Fig. 2); elytra darkly colored, at least basally; Venezuela 2
- Mesosternal process carinate (Fig. 4); pubescence of hind femur more developed, absent only in apical $\frac{1}{4}$; elytra testaceous; Middle America 3
2. Elytra piceus *liparus* Spangler
- Elytra with reddish brown fascia at base, remainder testaceous *rosalesi* Spangler
3. Head punctation finer and sparser, punctures separated by about 5 times their width; size larger, about 1.10 mm; aedeagus as illustrated (Fig. 5); Mexico *mexicanus* n. sp.
- Head punctation coarser and denser, punctures near eyes separated by their width, others by 3–4 times their width; size smaller, about 1.00 mm; Guatemala and Panama 4
4. Aedeagus as illustrated (Fig. 6); Guatemala *nucleus* n. sp.
- Aedeagus as illustrated (Fig. 7); Panama *tricarinatus* n. sp.

Notionotus mexicanus Perkins, n. sp. (Figure 5)

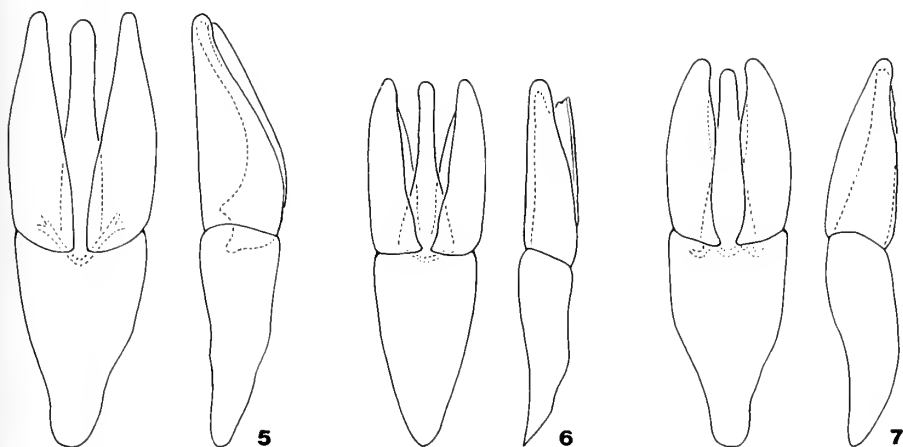
Type-data.—*Holotype* (male). Mexico, Oaxaca, 8 miles E. Tapanatepec, tropical stream with large boulders, 3-VII-1974, M. E. and P. D. Perkins. Deposited in the National Museum of Natural History, Smithsonian Institution.

Paratype.—(1 female). Same data as holotype.

Diagnosis.—This species is slightly larger than *nucleus* and *tricarinatus* (1.10 vs. 1.00 mm), has the head punctation distinctly finer and sparser than those species, and differs in aedeagal form (Figure 5).

Description of holotype.—Length 1.10 mm, greatest width 0.65 mm at midlength. Color testaceous dorsally except for brown between eyes and two small black spots near hind margin of pronotum, separated by about $\frac{1}{3}$ width of pronotum; mouthparts, antennae and most of legs testaceous, remained of venter reddish brown.

Head shining, finely sparsely punctate, punctures separated by 5 times their width. Clypeus expanded and shelflike in front of eyes, covering most



Figs. 5-7. *Notionotus* aedeagi, holotypes (dorsal and lateral views). 5, *mexicanus*; 6, *nucleus*; 7, *tricarinatus*.

of labrum, very finely alutaceous along anterior margin. Labrum shallowly emarginate medially. Ventral surface of head finely alutaceous behind eyes and in gular region; mentum shiny, finely punctate.

Pronotum almost 2.5 times as wide as long; punctures finer and sparser than those on head; narrowly margined laterally; anterolateral and posterolateral angles rounded. Prosternum longitudinally carinate in midline, acutely angulate at apex. Prosternal process distinctly produced posteriorly, distinctly separating front coxae; apex concave for reception of mesosternal protuberance.

Elytra convex, narrowly margined laterally; widest at anterior $\frac{1}{4}$, extremely finely sparsely punctate similar to pronotum. Sutural stria absent. Scutellum a small equal-sided triangle. Epipleura almost vertical.

Mesosternum with prominent triangular protuberance whose midline is carinate and on same plane as metasternum. Metasternum smooth and impunctate on swollen medial region, medial region lacking pubescence, adjacent lateral areas with sparse, rather long pubescence; apex of medial region broad between mesocoxae. Abdominal sterna finely alutaceous and moderately densely covered with short pubescence; last segment with a group of tiny golden setae set in small apicomedial emargination.

Front legs with femora pubescent along lower margin in basal $\frac{2}{3}$, upper margin alutaceous in basal $\frac{2}{3}$, apical $\frac{1}{3}$ smooth and shiny. Middle and hind legs alutaceous and pubescent in basal $\frac{4}{5}$, apical $\frac{1}{5}$ smooth and shiny.

Variation.—The single female known has the pubescence at the borders of the swollen medial area of the metasternum shorter and sparser than the holotype.

Distribution.—Currently known only from the type-locality in southernmost Oaxaca, Mexico.

Notionotus **nucleus** Perkins, n. sp.

(Figures 3, 4, 6)

Type-data.—*Holotype* (male). Guatemala, Alta Verapaz, 5 miles W. La Tinta, small tropical brook, 6-VI-1974, M. E. and P. D. Perkins. Deposited in the National Museum of Natural History, Smithsonian Institution.

Paratypes.—(4 males, 7 females). Same data as holotype, deposited in NMNH and the author's collection.

Diagnosis.—Distinguished from *mexicanus* by its slightly smaller size, more strongly punctate head, and aedeagus (Figure 6). Aedeagal form must be used to differentiate *nucleus* and *tricarinatus*.

Description of holotype.—Length 1.00 mm, greatest width 0.60 mm at midlength. Color testaceous dorsally except for brown between eyes and two small black spots near hind margin of pronotum, separated by about $\frac{1}{3}$ width of pronotum; mouthparts, antennae and most of legs testaceous, remainder of venter reddish brown.

Head distinctly punctate, some punctures near eyes separated by only their widths, others by 3–4 times their width. Clypeus expanded and shelf-like in front of eyes, covering most of labrum, very finely alutaceous along anterior margin. Labrum shallowly emarginate medially. Ventral surface of head finely alutaceous behind eyes and in gular region; mentum shiny, finely punctate.

Pronotum almost 2.5 times as wide as long; punctures finer and sparser than those on head; narrowly margined laterally; anterolateral and posterolateral angles rounded. Prosternum longitudinally carinate in midline, acutely angulate at apex. Prosternal process distinctly produced posteriorly, distinctly separating front coxae; apex concave for reception of mesosternal protuberance.

Elytra convex, narrowly margined laterally; widest at anterior $\frac{1}{4}$, extremely finely sparsely punctate similar to pronotum. Sutural stria absent. Scutellum a small equal-sided triangle. Epipleura almost vertical.

Mesosternum with prominent triangular protuberance whose midline is carinate and on same plane as metasternum. Metasternum smooth and impunctate on swollen medial region, medial region lacking pubescence, adjacent lateral areas with sparse, rather long pubescence; apex of medial region broad between mesocoxae. Abdominal sterna finely alutaceous and moderately densely covered with short pubescence; last segment with a group of tiny golden setae set in small apicomедial emargination.

Front legs with femora pubescent along lower margin in basal $\frac{2}{3}$, upper



Fig. 8. Biotope of *Notionotus mexicanus*, Mexico, Oaxaca, 8 miles E. Tapanatepec.

margin alutaceous in basal $\frac{2}{3}$, apical $\frac{1}{3}$ smooth and shiny. Middle and hind legs alutaceous and pubescent in basal $\frac{4}{5}$, apical $\frac{1}{5}$ smooth and shiny.

Variation.—The 12 specimens studied were quite homogeneous.

Distribution.—Currently known only from the type-locality in southeastern Guatemala.

Etymology.—Latin, *nucleus*, kernel. I refer to the small size, smooth convex dorsum and testaceous color of this species, and also to its distribution in the region known biogeographically as “nuclear” Middle America.

Notionotus tricarinatus Perkins, n. sp.

(Figure 7)

Type-data.—*Holotype* (male). Panama, Canal Zone, Albrook Forest Site, 22-III-1968, R. S. Hutton. Deposited in the National Museum of Natural History, Smithsonian Institution.

Paratypes.—(6 males, 10 females). Same data as holotype, deposited in collections of NMNH, David C. Miller and author.

Diagnosis.—Smaller and with punctuation of the head more developed than *mexicanus*. Aedeagal form (Figure 7) must be used to reliably differentiate *tricarinatus* and *nucleus*.

Description of holotype.—Length 0.98 mm, greatest width 0.55 mm at midlength. Color testaceous dorsally except for brown between eyes and two small black spots near hind margin of pronotum, separated by about $\frac{1}{3}$ width of pronotum; mouthparts, antennae and most of legs testaceous, remainder of venter reddish brown.

Head distinctly punctate, some punctures near eyes separated by only their width, punctures near midline separated by 3–4 times their width. Clypeus expanded and shelflike in front of eyes, covering most of labrum, very finely alutaceous along anterior margin. Labrum shallowly emarginate medially. Ventral surface of head finely alutaceous behind eyes and in gular region; mentum shiny, finely punctate.

Pronotum almost 2.5 times as wide as long; punctures finer and sparser than those on head; narrowly margined laterally; anterolateral and posterolateral angles rounded. Prosternum longitudinally carinate in midline, acutely angulate at apex. Prosternal process distinctly produced posteriorly, distinctly separating front coxae; apex concave for reception of mesosternal protuberance.

Elytra convex, narrowly margined laterally; widest at anterior $\frac{1}{4}$, extremely finely sparsely punctate similar to pronotum. Sutural stria absent. Scutellum a small equal-sided triangle. Epipleura almost vertical.

Mesosternum with prominent triangular protuberance whose midline is carinate and on same plane as metasternum. Metasternum smooth and impunctate on swollen medial region, medial region lacking pubescence, adjacent lateral areas with sparse, rather long pubescence; apex of medial region broad between mesocoxae. Abdominal sterna finely alutaceous and moderately densely covered with short pubescence; last segment with a group of tiny golden setae set in small apicomedial emargination.

Front legs with femora pubescent along lower margin in basal $\frac{2}{3}$, upper margin alutaceous in basal $\frac{2}{3}$, apical $\frac{1}{3}$ smooth and shiny. Middle and hind legs alutaceous and pubescent in basal $\frac{4}{5}$, apical $\frac{1}{5}$ smooth and shiny.

Variation.—Some specimens are brownish dorsally.

Distribution.—Currently known only from the Canal Zone, Panama.

Etymology.—Latin, *tricarinatus*, in reference to the tricarinate mesosternal protuberance.

Acknowledgments

I thank my wife Maureen for assistance with fieldwork in Mexico and

Guatemala. I am grateful to David C. Miller for the opportunity to study specimens from Panama. Thanks are due technicians of the Scanning Electron Microscope Laboratory, Smithsonian Institution, for taking the micrographs. Paul J. Spangler kindly reviewed the manuscript. Travel funds for fieldwork in Middle America were provided, in part, by the Smithsonian Institution.

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REVIEW: TABANIDAE OF THE EAST COAST
AS AN ECONOMIC PROBLEM

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Abstract.—Tabanidae are pests of man and animals in many areas of the coastal states but especially near salt marshes. The major species, *Tabanus nigrovittatus* and *Chrysops atlanticus*, move from the marshes to nearby beaches, camp grounds, golf courses, and other recreational areas and onto boats in the bays and estuaries. *Chrysops* congregate in dense vegetation and attack when humans or animals move into such places. Both *Tabanus* and *Chrysops* are severe problems to agricultural workers when the flies are numerous. Livestock are readily attacked by Tabanidae with consequent effects on thriftiness, weight gains and milk production and possible transmission of causal agents of disease. Biology and habits of both salt marsh and upland species are poorly known. Probably *T. nigrovittatus* is a species complex. Controls are inadequate though traps and vegetative barriers have been shown useful against *Tabanus* and some insecticides have given reduction but not adequate control of both *Tabanus* and *Chrysops*.

When one thinks of the blood-sucking Diptera of the east coast one thinks first of mosquitoes as the major problem. However, in many areas 50 to 75 years of organized control programs have resulted in only sporadic mosquito annoyance. Other biting flies are then regarded as greater pests such as Tabanidae, both greenheads (*Tabanus*) and deer flies (*Chrysops*).

Tabanidae as Pests

The Tabanidae are selective feeders and only a few are important pests of humans. Especially the larger *Tabanus* seem to limit their attacks to large mammals. Only female Tabanidae take blood meals needed for maturation of eggs. Some species of both *Tabanus* and *Chrysops* are autogenous, the females depositing the first egg mass before seeking a blood meal. Nutrients for normal fly activities are obtained from flowers and other plant sources or from food reserves stored in the larval stage.

The relatively few species of Tabanidae that bite man often occur in large

¹ Diptera: Tabanidae

² Paper of the Journal Series, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, New Brunswick, N.J.

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numbers and make life miserable. People feel the bite when the female pierces the skin or probes deeply for an adequate flow of blood. Usually no swelling, reddening or irritation occurs after the bite but some people have moderate reactions which last from a few minutes to several hours. A small segment of the population respond with allergic reactions involving extensive swelling, erythema, itching, and related effects. In extreme cases hospitalization is necessary and emergency measures to counteract allergic effects or anaphylactic shock are essential.

This tabanid problem is primarily associated with salt marshes, especially portions of *Spartina alterniflora* marshes. The most important fly in this area is the greenhead, *Tabanus nigrovittatus*, which often makes up 90 to 95% of the adult pest population.

The salt marsh tabanid problem extends from Nova Scotia to Florida and along the Gulf Coast to eastern Texas in areas of the salt marsh suitable to the various species or strains. Apparently suitable larval habitat for one strain of *T. nigrovittatus* exists only along banks of natural and mosquito control ditches (Freeman and Hansens, 1972).

Tabanus nigrovittatus females readily bite man and range quite widely from the salt marsh into nearby areas. Prevailing winds often favor infestation of beaches. Greenheads tend to fly within a foot or two of the ground, and thus on bathing beaches exposure of sun bathers results in maximum annoyance. A single bite often causes human response all out of proportion to the seriousness of the injury. Once the female fly settles down to feed, if one can wait that long, swatting the fly is easy. The wounds caused by tabanids are larger than those of other Diptera and blood often oozes from the wound after the fly leaves. If a larger blood vessel is pierced, bleeding may be profuse.

Occupants of fishing and pleasure boats are often attacked by greenheads. The flies readily move into the boat cabins as the vessels traverse the creeks and thoroughfares. These flies may then seek a host when the craft has moved a considerable distance from land. Flies may be attracted by petroleum products or the exhaust from gas engines. This accounts in part for the large numbers of greenheads which accumulate in power boats. Both sexes have recently been taken on oil drilling rigs in the Gulf of Mexico many miles from land and probably by direct flight from land (personal communication, John Burger, U. New Hampshire).

Golf courses in a number of localities have been constructed close to salt marshes. Vegetation may be cleared between the course and the marsh to give players a view of the wide expanse of the marsh. Observations show that such openings to the marsh greatly facilitate movement of flies to the course and subsequent annoyance of the players.

Campgrounds are a rapidly growing industry in coastal areas, especially in New Jersey. In Cape May County alone there are some 75 campgrounds.

Most of these are close to salt marshes and greenhead and deerfly annoyance is very severe. At one location in 1976 at least two children required hospital treatment for greenhead bites. At a number of locations, campers pulled stakes and left after a day or less of enduring greenheads and deer flies. This also happened on Grand Manan Island, New Brunswick, Canada (personal communication, L. L. Pechuman, Cornell Univ.).

An important problem with Tabanidae was apparent in South Carolina in the planning for the Charles Towne Landing Park in 1970 and a suitable control program was implemented (Adkins, 1974).

Greenheads have an impact on crop production in vegetable growing areas of New Jersey along Delaware Bay. In some locations intensive agriculture is surrounded on three sides by salt marsh and greenheads cause great annoyance to harvesting crews and other farm labor during much of July and August.

In other areas salt marsh has been reclaimed for housing by digging channels for boat moorings and raising adjacent land above high tide level with the spoil. Such marsh destruction removes greenhead breeding areas, but plenty of nearby marsh produces flies which easily infiltrate the developments.

Similarly the salt marsh deer flies, *Chrysops fuliginosus* and *C. atlanticus* are important pests of man. *C. atlanticus* is an avid feeder on man, exists in large numbers for several weeks, and reaches peak numbers when more people are in resorts and when crop harvesting is in progress. Along the South Atlantic coast other species are important especially in the Georgetown area of South Carolina where *C. pudicus* and *C. niger taylori* are pests (Adkins, 1974).

Human annoyance from *Chrysops* is restricted to smaller geographical areas than *Tabanus*. Deer flies from the salt marsh move into adjacent woods and other vegetation but not far into open fields. Typically they are not a problem on beaches or in boats but may be more serious than greenheads on golf courses, in camp grounds, parks, and along the wooded margins of cultivated fields. *Chrysops* tend to feed on the head and arms and are much more attracted to a moving host than one standing still. In the summer of 1976 at the margin of cultivated fields near Cedarville, N.J. as many as 180 *C. atlanticus* were taken in 10 figure-8 sweeps of an insect net over the head. With such a population, 30 actual bites were counted in 90 seconds, and observation for longer periods was unbearable.

So far reference has been made primarily to a small number of salt marsh species. There is a much larger fauna of Tabanidae in upland areas. *Chrysops* become pests in many local areas. *Chrysops vittatus* is probably the most generally distributed and hence the most annoying of the freshwater deer flies. Flies of the genus *Diachlorus* are avid biters and occasionally are important pests. Only a few species of upland *Tabanus* cause appreciable annoyance to humans.

In the Atlantic salt marsh areas, livestock production is not an important part of agriculture. The biting fly complex of mosquitoes, horse flies, deer flies, stable flies, and others greatly affects livestock thriftiness, weight gains and milk production. Granett and Hansens (1956) showed the cost of sprays on dairy animals was exceeded by increased return from milk production when blood-sucking Diptera were sharply reduced.

The amount of blood taken from livestock when *Tabanus* are present is considerable but depends on the species involved as well as the size of the population. Philip (1931) estimated a blood loss of 300 ml from a constant population of 50 flies feeding over a 10 hour period. Tashiro and Schwardt (1949 and 1953) similarly weighed engorged flies and calculated daily blood loss of 59 to 352 ml per day. Often even more blood is lost from the wounds the flies cause. In coastal areas, especially in the south, animals suffer large blood loss over several months because the fly population is very large and the fly season is prolonged. Soboleva (1956) reported loss of 40 to 200 mg of blood from feeding by a single fly and qualitative changes in blood with feeding of numerous flies, i.e. a decrease in haemoglobin and erythrocytes and an increase in leucocytes.

Disease Transmission

Active transmission of human disease agents by Tabanidae is not known to occur in the Atlantic coastal states. Possible exceptions are tularemia and the viruses of the California encephalitis group. Laboratory tests have recently demonstrated that *C. atlanticus* is an effective vector of the filarial worm *Loa loa* of Africa (Orihel and Lowrie, 1975) but introduction of the disease agent to the east coast seems unlikely.

An additional factor in livestock production is the known potential of *Tabanus* as mechanical vectors of bovine anaplasmosis, equine infectious anemia, and vesicular stomatitis (not proved) (Krinsky, 1976). Hog cholera transmission was shown by Tidwell et al. (1972). Research in New Jersey showed the populations of Tabanidae on hogs are small but the number of species which visit hogs is quite large (Weiner and Hansens, 1975). Hog cholera transmission by tabanids is believed to be insignificant but such rare occurrences may be very important in reaching our national goal of complete hog cholera eradication. Wildlife of several species are subject to trypanosomes and filarial worms transmitted by tabanids.

Control Efforts

Control of Tabanidae has yet to be achieved. A variety of measures now in use give partial control. For preventing biting of man and animals no satisfactory repellents exist though DEET and ethyl hexanediol give some reduction in *Chrysops* biting. Catts (1968) advocates use of repellent im-

pregnated shirts to reduce biting annoyance. Light colored clothing also helps reduce attacks from greenheads and deer flies (Hansens, 1947).

Insecticide applications have met with only limited success. The areas to be treated are large because large expanses of salt marsh are breeding areas for these flies and the adult flies move considerable distances. The vegetation where *Chrysops* concentrate is often difficult to penetrate with air application and is inaccessible from the ground. Concentrations of insecticide needed often exceed the amounts which are environmentally safe. Large scale control of *T. nigrovittatus* by chemicals is unlikely to be acceptable except in emergency situations. In the case of *Chrysops*, control in localized areas where flies concentrate is feasible. Synthetic pyrethroids with short residual activity may be useful. In 1976 in New Jersey treatment along the edges of fields with resmethrin sprays resulted in relief from deer flies for only a day or two (unpublished, Hansens). In recreational areas such applications might also reduce annoyance to tolerable levels.

Use of box and canopy traps for control of *T. nigrovittatus* has met with considerable success in Maine, Massachusetts, New Jersey and Delaware. Large numbers of box traps have been used in Massachusetts since 1967 to protect beach areas (Spencer, 1971), in New Jersey to reduce fly annoyance on a golf course adjacent to salt marsh, and in Delaware to protect a small community from fly annoyance. In New Jersey the traps were successful enough that one golf course now includes traps as part of their pest management program. In Massachusetts traps are operated by mosquito control agencies and are important in reducing annoyance on beaches, in marinas, on golf courses, and at horse shows. In Delaware box and canopy traps placed in flyways (openings through the barrier of vegetation along the marsh) prevented large numbers of flies from moving into inhabited areas. In all of these efforts traps do not eliminate flies but reduce them to tolerable levels. Canopy traps (personal communication, L. L. Pechuman) are being used in the Hudson Valley, N.Y. around paddocks where valuable stud horses are kept and where EIA is a problem. Horse breeders say they are a great help in reducing populations.

Flooding of breeding areas was shown to control *Chrysops* larvae in Connecticut (Anderson and Kneen, 1969) but extensive area control would destroy too much desirable salt marsh.

Research Needs

Effective control of the various tabanids on the Atlantic seaboard will be difficult to achieve without much more knowledge of the life history and habits of the flies and development of laboratory rearing technique. In the case of the salt marsh species, oviposition habits of *C. fuliginosus* are unknown. Oviposition and larval and pupal habits need more study with *T.*

nigrovittatus and *C. atlanticus*. A recent paper by Magnarelli & Anderson (1977) adds considerable knowledge relative to feeding and gonotrophic activity.

Taxonomic and biological research is needed to clarify the *T. nigrovittatus* complex. The recognition by Freeman and Hansens (1972) of two distinct larvae in two distinct habitats on the salt marsh led to the reasoning that *T. nigrovittatus* populations may be of two species which are difficult to separate as adults. The second species is probably *T. simulans* and the two species overlap in Delaware and New Jersey. We also know that many fewer of the so-called *T. nigrovittatus* are taken in box traps in North and South Carolina than in Delaware and New Jersey. *T. nigrovittatus* also is not as serious a pest of man in the Carolinas as it is farther north. All of this gives credence to the idea that a species complex exists.

In general, adequate regional keys to adults are available for both salt marsh and upland species. Keys to larvae are less complete. Our big gaps in knowledge are in biology and habits and in establishment of a laboratory colony of any species. When these are known, new approaches to control will follow. Development of adequate controls will then make life much more enjoyable in many resort and agricultural areas of the east coast.

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NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVII(4), 1979, p. 319

BOOK REVIEW

Viroids and viroid diseases. T. O. Diener. John Wiley & Sons. 252 pp. 1979. \$19.95.

What are viroids? The subject, and the name, might be unfamiliar to many, because the study of viroids began in the present decade. Quoting from the preface of this volume: "Viroids are the smallest known agents of infectious disease. They are responsible for a number of destructive diseases of cultivated plants, but may also occur and cause disease in animals. Although some of the diseases that viroids cause had been known for decades, these diseases were generally believed to be due to infection by conventional viruses. The unique nature of their causative agents came to light only in 1971" The author of this volume is the foremost authority and the actual discoverer of viroids, who has coined the name "viroid" for these small nucleic acid molecules. The interest in viroids is not limited to plant pathologists, and it seems likely that diseases of insects and of higher animals will be recognized as caused by these agents, once the techniques, clearly described in this volume, will be applied more widely to the study of "uncertain etiology" ailments. Diener has provided a remarkably comprehensive, unified, and well-written volume on all aspects of viroids. There is no other book available that successfully covers this range of material. The introductory chapter presents the chronology of discoveries that resulted in the convincing evidence that viroids consist of nonencapsulated nucleic acid, that the infectious process is not caused by a contaminating virus, that viroids contain a low molecular weight nucleic acid that replicates autonomously without a helper virus, and consists of one molecular species only. At present (1979) seven viroids have been recognized, all causing plant

diseases of economic importance. The author discusses the widespread nature of established viroids and their serious potential threat to agriculture. He also provides a very stimulating discussion of future research problems and approaches, including the intriguing possibility that certain "slow viruses" causing human diseases might actually be caused by viroids. Although the primary audience for this book will consist of plant pathologists, medical and veterinary researchers, virologists, and molecular biologists, many entomologists, particularly insect pathologists will find this subject of considerable interest. The exhaustive bibliography and subject index, totaling 27 pages, add to the value of this definitive treatise. The book is a joy to read and it will be valuable for many years to come both as a text and a reference.

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NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVII(4), 1979, p. 320

BOOK REVIEW

Twelve Little Housemates. Karl von Frisch. Pergamon Press, Oxford, New York. 1979. 155 pp. \$12. Hard cover; \$6. Paperback.

The 4th (1955) German edition of the popular book by Nobel laureate Karl von Frisch has been translated into English in 1960 and reprinted several times. Now the enlarged and revised English edition has been published for the Pergamon International Library of Science. The book is written for lay people in a non-technical, humorous style and it is intended for the general public. Although not specifically aimed at entomologists, it nevertheless belongs to the personal library of every entomologist. The 12 invertebrate "housemates" are the housefly, gnats, the flea, the bed bug, lice, the clothes moth, the cockroach, aphids, ants, silverfish, spiders and ticks. The book was aimed primarily at the European reader and the author did not include termites, practically unknown in Central Europe, but of considerable importance in other parts of the world. Here are samples of some subtitles: "How to recognize a fly"; "How flies help doctors"; "How one can get lice, and how to get rid of them by methods other than those of gas warfare"; and on cockroaches: "Mouths that bite, lick, suck and sting." The book is enjoyable and educational not only for children but also for adults, including scientists.

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NEW YORK ENTOMOLOGICAL SOCIETY
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BOOK REVIEW

Peru, My Unpromised Land. Felix Woytkowski. 232 pp. Published for The Smithsonian Institution and NSF by National Center for Scientific, Technical and Economic Information, Warsaw, Poland, 1978. Available from U.S. Department of Commerce, NTIS, Springfield, VA 22161. (PB295870T) \$12.00.

This is a fascinating account of entomological and botanical explorations made in Peru by the Polish collector Felix Woytkowski during the years 1929-1964. The book was published first in Polish in 1974 and it was now translated into English. The highly readable volume opens with a description of the author's early memories of his childhood and life in Southeastern Poland (now Soviet Western Ukraine) and his educational and family background. As a son of a physician, Woytkowski obtained a thorough training in Poland and Western Europe, including a period spent in Oxford, England. In 1929 he was lured by an advertisement to leave a rather well paid position and to go to Peru, where he was promised free passage, tools, and a home-stead farm. Upon arrival, he found none of the promised benefits and was placed in a shanty immigrant camp with hundreds of French, Belgian and German immigrants who had been waiting for many months to be transported to the "free farmland." Finally many of the immigrants were able to return to their countries of origin, but Woytkowski decided to stick it out and to remain in Peru. He began to collect insects and medicinal plants, and to ship them to taxonomists in the United States. The second part of the book covers the years 1937-1951, a period during which he suffered hunger and pain, lost his only son and was abandoned by his wife, but did not give up the profession that gave him the only satisfaction in life. His unusual courage and perseverance helped him to overcome the incredible obstacles facing a stranger in the remote areas of Peru.

Numerous, life-long friendships with U.S. entomologists sustained Woytkowski through the most difficult years of deprivation. Many of his "clients" were members of the N.Y. Entomological Society and among his best friends were Charles P. Alexander, F. Martin Brown, J. Douglas Hood, Leonora W. Gloyd and Herbert B. Hungerford. His fondness for traveling and enthusiasm guided him throughout his life. Interested in nature and people, he struggled to survive in a hostile environment, finding new and rare species of insects and supported morally and financially by prominent entomologists. His family life was an unhappy one and his dream to discover the mysterious "Callanga" of Peru was never fulfilled.

The third part of the volume describes exporitions from 1951 to 1965 in the valley of the Costripata River, the jungle of the Madre de Dios basin, the search for medicinal plants, and encounters with hostile Indians in the

little-explored interior of Peru. Several years ago F. Martin Brown wrote: "Woytkowski had been a hero in the domain of natural science, about whom no books were written so far" The present account, in the style of a narrative by Woytkowski, actually has been written by M. Salomea Wielopolska, who was able to assemble not only his letters, photographs and notes, but also obtain additional information from entomologists who had close contacts with Woytkowski. Consequently, the account is vivid, often frightening, describing the dangers and deprivations of one of the most devoted collectors of recent years. The book ends with an epilogue and a chronological list of expeditions. After 36 years in Peru, Woytkowski, by then an old and sick man, found that he could not qualify for a small pension from the Botanic Garden in Lima, because he never became a Peruvian citizen. He decided to return to his native Poland, now a different and strange country to him, where he suffered not only because of the cooler climate and conditions, but, as he wrote, "because I found myself in a situation in which I could be useful and constructive no longer." He died in Krakow, Poland, in 1966.

The English translation of the Polish text is good; numerous black and white photographs taken by the author illustrate the localities and people of Peru's seldom visited mountains and valleys. There are 6 charts of the areas explored in the years 1930–1964. The book is much more than a travelogue—it is the account of a naturalist's life and hardships and of a devotion to entomology that will appeal to professional and amateur collectors alike. The information will be of special interest to anyone concerned with the culture and the people of Peru. The author's insight and the description of problems encountered during his explorations might help future collectors.

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NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVII(4), 1979, pp. 322–323

BOOK REVIEW

Ecological Methods, With Particular Reference to the Study of Insect Populations. T. R. E. Southwood. Second ed. Chapman & Hall-Halsted Press-John Wiley and Sons, New York. 524 pp. 1979. \$25.

The popularity of this book is evidenced by the fact that, after its publication in 1966 and reprinting in 1968, it has been reprinted in 1971, 1975 and 1976, before the present, revised edition first appeared in Cambridge, England in 1978. The reason for the popularity of this scholarly treatise can be found in the remarkable developments in the science of ecology. Ecologists need reliable quantitative data which this study contains. Written in a charming style, it gives a complete account of the theory and applications

of the subject. The chapters deal with the study of animal populations, the sampling, description of dispersion, absolute population estimates using marking techniques, sampling a unit of habitat, such as air, plants, plant products and vertebrate hosts, soil, litter and fresh-water habitats. Methods of population measurement, estimation of natality, mortality, and dispersal, are described in depth. Entomologists will be particularly interested in the discussion of age-grouping of insects, time-specific life tables and predictive population models. An author index and a general index are provided. Needless to say that this is a most useful book which will reward the individual reader and will also serve as a textbook. The book is technically excellent and its wide scope and lucidity make this new revised editin well worth having wherever ecological problems are being studied.

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BOOK REVIEW

Arthropod Phylogeny. A. P. Gupta, editor. Van Nostrand Reinhold. 762 pp. 1979. \$32.50.

This book provides a much needed up-to-date review of the growing body of information on the phylogeny of arthropods. Written by 13 scientists who have made many significant contributions to our knowledge of arthropods, this is a well organized, well illustrated, and clearly written book. The chapters deal with the morphology of fossil arthropods, early and late embryonic stages, abnormal metamorphosis, evolution of antennae and scent detection mechanism, eye structure, functional morphology and evolution of hexapods, arthropod visceral anatomy, intersegmental tendon system, sperm transfer and ultrastructure, neuroendocrine structures, and hemocytes. Several chapters are of special interest because of the well-organized and thorough treatment of their topics. Gupta's chapter on types of arthropod hemocytes in various arthropod groups and his penetrating analysis how they relate to arthropod phylogeny and evolution in general, as well as K. V. Clarke's presentation of the visceral anatomy and arthropod phylogeny are real masterpieces. Other topics are also treated exceedingly well. A taxonomic and a subject index are provided. I am convinced that the quality of this treatise will establish this book as a standard reference work and an essential addition to all scientific and biological libraries.

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BOOK REVIEW

Recent Advances in Acarology. I. J. G. Rodriguez, editor. Academic Press.
631 pp. 1979. \$35.00.

This volume (I) of the proceedings of the V International Congress of Acarology contains 80 reports given at the congress in August 1978. The book is divided into 6 parts: pest management of agricultural mites; biology of spider mites; stored product acarology; physiology, biochemistry and toxicology; ecology and bionomics; and recent advances in soil mite biology. The volume fills a gap and its prompt publication will be most welcomed by all interested in mite and tick research. The book has contributions from an international group of congress participants, including world authorities as well as young researchers. Careful editing resulted in a very readable volume. The book will be of special interest to mite specialists, entomologists, graduate students, teachers, researchers and practically oriented agricultural experts. The volume lacks a subject index.

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HONORARY LIFE AND SUSTAINING MEMBERS

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INDEX TO SCIENTIFIC NAMES OF ANIMALS AND PLANTS

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